

B

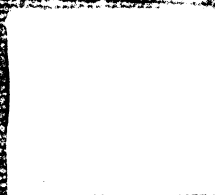
UNIVERSITY

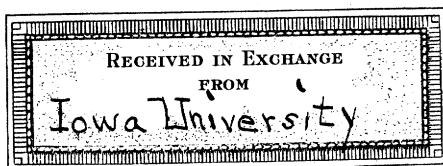
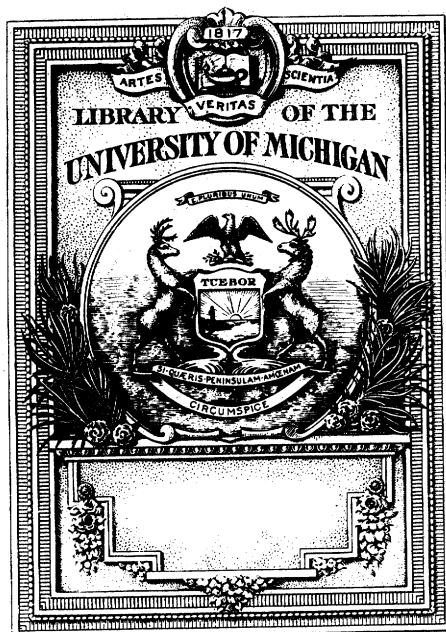
STUDIES

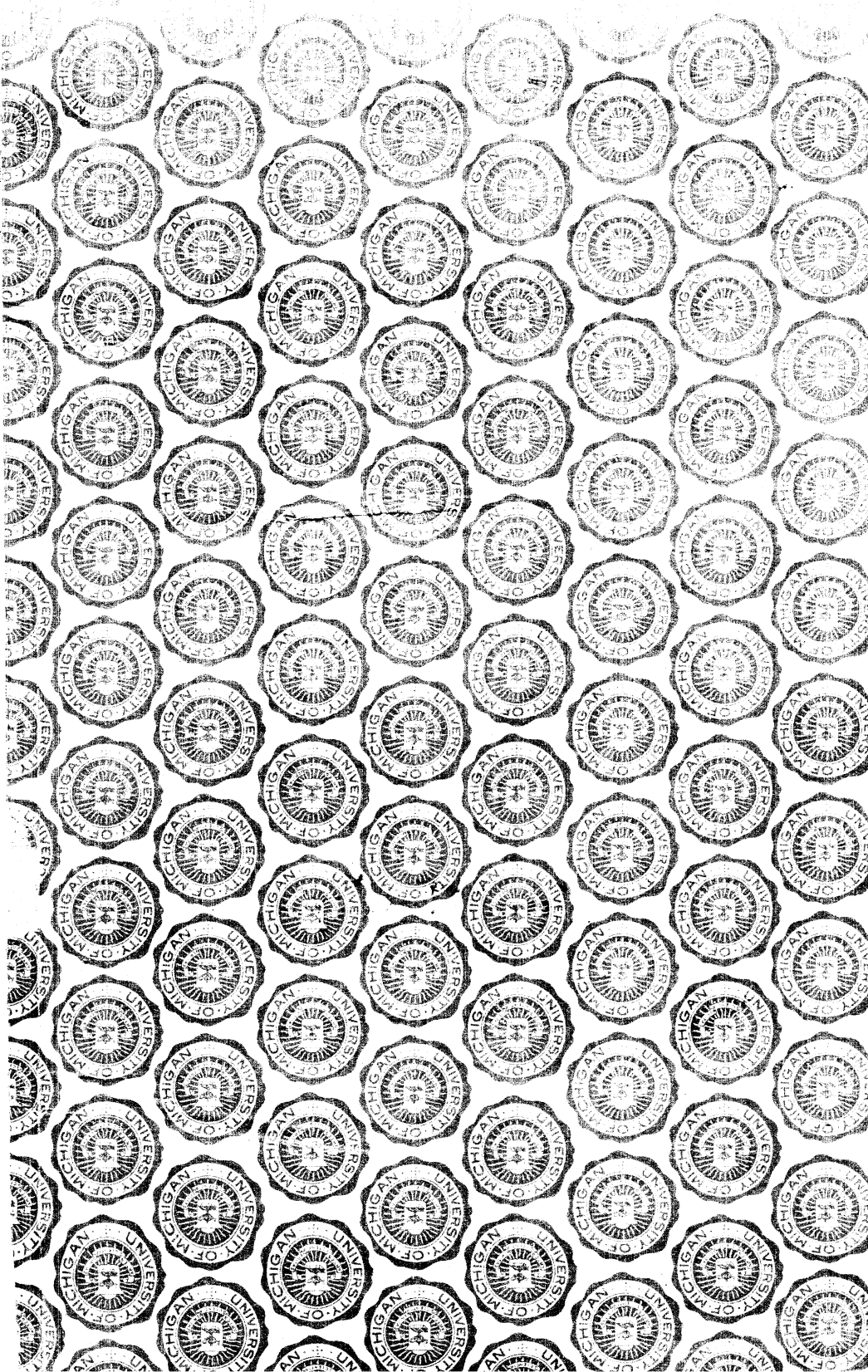
NATURAL

HISTORY

1025-27







QH

1

I64

UNIVERSITY OF IOWA STUDIES
IN NATURAL HISTORY

VOLUME XI
1925-1927



CONTENTS

- No. 1 FITZPATRICK, F. L. Ecology and economic status of
citellus tridecemlineatus
- No. 2 HORSFALL, J. L. Life history and bionomics of *aphis*
rumicis
- No. 3 DE RYKE, WILLIS. The development of the renal por-
tal system in *chrysemys marginata belli* (Gray)
- No. 4. MANN, W. M., VIERECK, H. L., ALEXANDER, C. P.,
WENTWORTH, C. K. Entomological and geological
papers
- No. 5 SHIMEK, BOHUMIL. Papers on the prairie
- No. 6 BYERLY, T. C. The myology of *sphenodon punctatum*
- No. 7 MORTENSEN, TH., DEICHMANN, ELISABETH, LINDSEY, A.
W. Echinoderms and insects from the Antilles
- No. 8 THOMAS, A. O., LADD, H. S., LUGN, A. L. Papers on
geology
- No. 9 JONES, D. T., POTTER, G. E., MARSHALL, RUTH. Fresh-
water fauna of Iowa
- No. 10 WINTERS, GRACE and LOHMAN, M. L. Papers on Iowa
fungi
- No. 11 WENTWORTH, CHESTER K. Methods of mechanical an-
alysis of sediments
- No. 12 LARRABEE, AUSTIN P. An ecological study of the fishes
of the Lake Okoboji region

UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

VOLUME XI

NUMBER 1

THE ECOLOGY AND ECONOMIC STATUS OF CITELLUS TRIDECEMPLINEATUS

by

FREDRICK L. FITZPATRICK

PUBLISHED BY THE UNIVERSITY, IOWA CITY

INTRODUCTION

Citellus tridecemlineatus tridecemlineatus was first described by Dr. S. L. Mitchill, who gave it the common names "Thirteen-lined Ground Squirrel" and "Federation Ground Squirrel." The latter name was applied because of a fancied resemblance to thirteen lines of stars and stripes. (S. F. Baird, 1859, p. 316). The scientific name first applied by Mitchill in 1821 was *Sciurus tridecemlineatus*. The same species has likewise been referred to as *Spermophilus tridecemlineatus*. At present it is recognized as belonging to the genus *Citellus* and the species is divided into geographical races.

Various common names for this animal have been developed locally. Among them are the following: "Striped Prairie Squirrel," "Picket-pin," "Striped Gopher," "Striped Spermophile," "Striped Ground Squirrel," "Thirteen-lined Spermophile." Only the last two of these names are in any way suitable, for the rest tend to cause confusion with other species.

This rodent was selected as a problem for study because very little concrete scientific investigation has been made with regard to its habits. An examination of the bibliography will show that while a number of authors have touched upon the subject, the work has been universally general and may usually be summed up in one or two pages. In fact this species has not previously been the subject of a detailed general examination. All of the works cited, however, have some bearing on the problem and have been of value in its development.

Two spermophiles occur commonly in Iowa: *Citellus tridecemlineatus tridecemlineatus* (Mitchill), and a larger species, *Citellus franklini* (Sabine). They vary in abundance locally, but the first named form usually predominates in numbers and is therefore of most interest from an economic standpoint.

The economic status of *Citellus tridecemlineatus tridecemlineatus* has been a subject of discussion for some time. Certain counties have even gone so far as to offer a bounty for this species, but such plans proved impractical, resulting in too heavy drains on county funds.

Three general methods were employed in the course of this work.

In the first case the animals were observed as to habits and general characteristics both in the field and in captivity. Then specimens were collected at different times of the year and studied as to parasites, stomach contents, and embryonic development. Finally, a large number of burrows were excavated, the results of this work being chronicled farther on. The investigations were carried on in different localities, and an attempt was made to include extremes of environment. With this in view the writer has made a number of trips to different parts of the state.

Some difficulty has been encountered in treating this subject coherently, for the habits are in every case dependent upon environment.

Before closing the introduction the writer wishes to express his indebtedness to Professor Henry F. Wickham for continuous aid and direction in the pursuit of this work. And also to Professors C. C. Nutting, H. R. Dill, and Dayton Stoner for encouragement and helpful suggestions.

A somewhat different acknowledgment is made in the case of Mr. R. A. Brown of Des Moines, who in the summer of 1922 made a collecting tour over the northern part of Iowa in company with the writer, and who proved to be of material aid in the securing and preservation of stomach contents.

GENERAL HABITS AND ENVIRONMENTAL CONDITIONS

DISTRIBUTION

Citellus tridecemlineatus tridecemlineatus occurs generally in the upper Mississippi valley from Ohio west to the plains, and from Missouri and Illinois northward into Minnesota, Wisconsin, and Michigan. To the westward this species is replaced by *Citellus tridecemlineatus pallidus*, which form is very similar in size and habits but somewhat lighter in coloration.

Iowa is almost in the center of the range covered by the Thirteen-lined *Spermophile*. Reports from all parts of the state point to a practically uniform distribution, the animals being common residents in most cases. The writer has selected the following counties as examples of areas in which this species is particularly abundant: Clay, Dickinson, Emmet, Iowa, Jones, Louisa, Pocahontas and Polk. It must be remembered, however, that abundance in any locality is variable, being dependent on an ever fluctuating environment.

GENERAL CHARACTERISTICS

The Thirteen-lined *Spermophile* has a number of well defined habits. One of these is the characteristic attitude assumed when listening or attracted by approaching objects. The animals sit on their hind legs in an erect position which has gained for them the colloquial term "Picket-Pins." Undeniably curious in the presence of man these *spermophiles* will assume the erect attitude and stare at the intruder for an indefinitely long period of time. When crowded too closely they race rapidly to their holes and take immediate refuge. In the safety of their retreats they will often stick their heads out of the openings for brief intervals to watch the actions of their enemy, sometimes uttering their familiar call meanwhile, perhaps as a warning to other members of the species. They are quick and seemingly nervous in all of their actions.

The Thirteen-lined *Spermophile* is a strictly diurnal species. The animals prefer the warmer parts of the day for their activities above ground, particularly when the sun is shining. They come out of their retreats for successively shorter periods each day as the weather becomes colder.

The animals have a tendency toward colonialism and live in groups as a rule. Upland or lowland valleys with few or no trees are habitually inhabited by this species. Areas where the grass has been closely cut down by stock or where the short white clover dominates over the taller blue-grass are preferred, for, as will appear later, the animals are partially dependent upon the insects which they capture for food, and in the tall vegetation they would be at a great disadvantage. Heavy timberlands are not frequented although in open wood-lots there may be occasional burrows. *Spermophiles* are apparently independent of ponds and creeks for their water supply for their holes are often found on the crests of high broad divides. This particular subject, however, will be more fully treated in the succeeding chapter.

These *spermophiles* are not pugnacious as a rule. They usually take refuge by retreat into a burrow when an enemy approaches. The males engage in minor battles among themselves during the mating season, but the injuries sustained are usually negligible. (Stoner, 1918, p. 131).

SPRING APPEARANCE AND MATING

The first Thirteen-lined *Spermophiles* appear above ground between the fifteenth of March and the tenth of April, depending on the season. By this time all of the frost has been thawed out and the weather is reasonably mild. Their advent is usually preceded by several warm sunny days, but if the temperature falls the *spermophiles* will again become inactive until the weather moderates.

Mating does not take place immediately, but is deferred until about the second or third week in April. During the mating season the animals are unusually active and spend the greater part of the day above ground. They are conspicuous at this time of the year, as they call back and forth continually. The males engage in occasional fights for the possession of mates.

NESTS AND YOUNG

During the first week in May, females may often be observed re-excavating old burrows. If killed at this time a dissection will generally reveal the presence of well developed embryos. Some new burrows are constructed, but as a rule tunnels are merely hollowed out and new nests built. Dead grasses of the preceding year are used in the construction of these nests. Further information on this subject is contained in Chapter II. Dissection has shown that

not all of the females are fertilized and in one instance the writer detected a diseased condition of the developing embryos.

There is great variation in the number of young produced. Adult females of the preceding year show a general tendency toward having fewer offspring than the older females. They may be as few as four or as many as ten in number. Cory (1912, p. 141) quotes Dr. Hoy to the effect that the young are naked at birth, blind and remarkably embryonic. They do not have hair until they are twenty days old and the eyes do not open until the thirtieth day. During this period they are fed and otherwise cared for by the female. Much insect food is carried to the young.

About the middle of July, two-thirds grown young appear at the surface of the ground and begin to capture or otherwise secure their food. Some of them begin to dig out new burrows, some remain in the parental burrows, and still others wander to old unoccupied burrows or retreats in the near vicinity. The relative quiet of the reproductory season is broken now and the members of the species again resume their former habits.

It is well established that the males leave the females, or are driven off during the season when the young are produced, and assume wandering habits, going from place to place in search of food, and incidentally constructing many new retreats in the process of their travels.

LOCAL MIGRATION IN SEARCH OF FOOD

The activities of mating are carried on for the most part in the immediate vicinity of the place where the animals have hibernated. After mating, however, the individuals and particularly the males, tend to spread out in search of the most advantageous feeding grounds. Old outlying burrows at the borders of fields and along roadsides or in small isolated patches of grass are now reoccupied.

Early in the summer newly planted corn may be attacked to some extent, the amount of actual damage depending upon the number of spermophiles in the vicinity and the presence or lack of other foods. This particular topic will be developed under "Food Habits."

The writer has seen these spermophiles leave rather large areas entirely, during seasons when they were not being pastured and the grass had become long. For as previously explained, the short grass is of advantage to the species, and if it becomes tall in any locality there will be a forced migration of the spermophiles. This

is a general rule in regard to local distribution, but there are some few cases on record where spermophiles remained far out in hay-fields during the early part of the summer when the grass averaged as much as a foot in height. Here they were no doubt practically dependent on vegetable foods.

Thirteen-lined Spermophiles will immediately encroach upon newly-mown fields where many insects are easily accessible on the fallen hay and grain. Here they will remain for a week or more, constructing shallow burrows into which they retreat at night or when threatened by any of their various natural enemies.

The abundance of natural enemies tends to affect distribution somewhat. For instance, a whole pasture may be depopulated of spermophiles by the attacks of a single Cooper's Hawk.

STORING OF FOOD

Thirteen-lined Spermophiles seem to have a rather moderately developed instinct to store food materials in their underground retreats. Such a practice is not essential, however, and is not resorted to in the majority of cases. The writer has found small caches of grain, principally corn, on several occasions. In some cases it seems that the food was stored in the fall and remained untouched until the following spring when the spermophiles came out of hibernation.

G. E. Johnson (1917, pp. 267-68) reports the following case in regard to storage of food: "The burrow occurred in a pasture near Canistota, S. Dak., fifteen rods from an oat field. The first nest was about two feet from the outside opening, the entrance running back under the first part of the burrow. This nest was filled entirely full with unshelled oat kernels and a little dry grass. The estimated number of seeds by counting one-sixteenth of them was 23,000 to 24,000. This nest was only seven inches below the surface of the ground, and may have been an emergency store-house. The second nest was about sixteen feet from the first, measuring along the burrow, and was twelve inches below the surface of the ground. It was seven inches in diameter. It contained a handful of dry grass and about 4,000 oat kernels unshelled." Further on in the same paper, Johnson records the storing of wheat kernels in a similar manner.

It is the opinion of the writer that grain is sometimes stored when it is plentiful and easily obtained. Such storages are used in case of emergency when other food supplies fail, as in the late sum-

mer and fall after a frost when the insects are few in numbers. The members of this species eat insects when they are available, but evidently store grain during the harvest season, even if it is not the principal article of diet at the time.

PREPARATIONS FOR HIBERNATION

The first indications of cold weather in the fall result in a marked diminishment of activities on the part of *Citellus tridecemlineatus tridecemlineatus*. Some warm days during September will find these spermophiles above ground. There is some excavation going on, as old burrows are deepened, and nests are lined with grass in preparation for the coming winter. No doubt the great majority of the species simply remain in the deepest burrows. However, the writer has noted cases where this species took over much larger abandoned burrows of other animals in the fall. In one case, a spermophile was observed carrying nest materials into the former den of a woodchuck, at Iowa City, September 14, 1922. There is no doubt that in some cases they prefer the deeper burrows of other animals during the winter season, and are in this manner enabled to retreat below the frost line.

All existing observations seem to point to the fact that each individual constructs a separate hibernating cell or nest. Further, but one animal hibernates in a burrow ordinarily. In one case two hibernating nests were found off the passages of a common tunnel, but they were some twenty feet apart.

Just before hibernation is entered upon, all the openings of the burrow are plugged with dirt for a distance of from one to three feet. If there is a succeeding period of warm weather, the plugs may be removed temporarily, but they usually remain until the following spring, practically obliterating the signs of the burrow's presence.

HIBERNATION

As has been inferred, the degree of activity shown by *Citellus tridecemlineatus tridecemlineatus* is directly dependent upon temperature. Warm sunny days find the spermophiles above ground and extremely active. On the other hand, they are equally inactive during cool rainy weather, even in mid-summer. G. E. Johnson (1917, p. 268) reports a variation of 4° C. in the temperature of an individual during a single day. This phenomenon is not uncommon among animals which "hibernate" in the true sense of the word.

After closing its burrow a Thirteen-lined *Spermophile* curls itself up in the nest previously prepared for that purpose and gradually passes into the torpid condition known as hibernation while the surrounding earth is becoming cold. If the *spermophile* be removed now into warmer surroundings it will gradually revive, but will become torpid again if restored to the colder medium. Experimentation has shown that if the temperature of the *spermophile's* body be reduced below the freezing point death will result in a short time.

The life processes of the *spermophile* must be sufficient to counteract the cold influence of the walls of the burrow, for the animal hibernates in a medium which is often well below the freezing point. On the other hand, the vital activities must be reduced sufficiently that they will not cause too heavy a drain on the animal's store of fatty tissue.

Previous investigations as to the actual organic conditions of hibernation have been successfully conducted by Dr. P. R. Hoy (1875, pp. 148-50), who reports the following interesting facts: The pulse is reduced from 200 to 4 beats per minute. Respiration is reduced from 50 to practically zero. Temperature falls from 105° F. to 58° F. Circulation is very feeble and amputation of a limb may be accomplished with very little loss of blood. There is a prominent congestion of blood in the thoracic region. There is no muscular response to stimuli, not even if a nerve be severed.

STRUCTURE OF BURROWS AND RETREATS

FOREWORD

The examination of many burrows by means of excavation has made clear to the writer that their construction is dependent on a large number of varying conditions. The different kinds of burrows it is true, fall roughly into two classes: permanent and temporary, but exceptions to even the most general types are met with on every hand. It may be said that the Thirteen-lined *Spermophiles* show a certain aptitude to take advantage of favorable conditions in connection with the construction of burrows. This fact alone would account for considerable diversity of structure since this species inhabits a variety of soils under many changing conditions of agricultural development.

A great many factors must be taken into account if an attempt is made to correlate the structure of any burrow with environmental circumstances. The kind of soil may be considered as a determining element. Drainage, elevation, accessibility of food, character of vegetation and the number and variety of natural enemies serve as similar influences. In many cases a certain type of structure may be traced back to certain combinations of these factors.

In Iowa, Thirteen-lined *Spermophiles* are found both in the valleys and on the uplands. They migrate back and forth locally in order to take advantage of abundant food supplies. As an example of this the writer has often noted that these animals are particularly abundant on newly raked hay fields. The reason of course is obvious. Many of the insects that live on the hay in the early months of the summer are now left on the short stubble where they come within reach of the *spermophiles*. Accordingly many *spermophiles* migrate in from adjacent pastures to take advantage of this easily obtained food.

The Thirteen-lined *Spermophiles* never venture far from an underground retreat of some sort and this habit or instinct leads them to construct new burrows or renew old ones whenever they encroach upon new territory. Such burrows are usually of a temporary nature, for in many cases the vegetation grows up later in the season and the *spermophiles* return to the pasture where

the grass is shorter. This general example is cited to indicate the multitude of conditions which may directly affect the habits of this species and indirectly affect the construction of its burrows.

Local migration explains many things in connection with burrows that would otherwise remain a mystery. It explains the fact that the number of burrows is relatively large in proportion to the number of individuals living in the vicinity. As a rule at least half of the burrows in a given region will be unoccupied although at any time they may become reinhabited. In this connection it is of interest to note that the spermophiles are usually found singly in separate burrows as indicated in the treatment of general habits. This habit would also tend toward the construction of a comparatively large number of burrows and no doubt is nearly as important a factor as local migration itself.

G. E. Johnson (1917, p. 264) writes with reference to the burrows of *Citellus tridecemlineatus tridecemlineatus* as follows: "Approximately fifteen of these burrows were in the sandy regions of South Chicago (Nov. 11) and were of one type, about two feet in length and eight to fourteen inches in depth, and showing no evidence of recent occupancy. . . . The remaining burrows were in sod (humus) with clay subsoil. These ranged from four to twenty feet in length and from four to forty-six inches in depth. Of the seventy-eight burrows measured, thirty-seven per cent were two feet or less in length and nine inches or less in depth; while sixty-seven per cent were four feet or less in length and thirteen inches or less in depth; and only fourteen per cent were longer than six feet or deeper than seventeen inches."

The first burrows, referred to as being in the sandy region about Chicago, are no doubt examples of temporary structures which had been in use during the summer as a result of local abundance of food. As winter approached (remembering that there is little activity among the members of this species after the first of November) the spermophiles would naturally withdraw to older, deeper burrows, leaving the former in the unoccupied condition that they were found by Mr. Johnson. The last part of the quotation is included to substantiate a point brought out in the preceding pages; that there is a great variety of burrow structure and that there are many small temporary burrows in proportion to the number of long permanent tunnels. It will be observed that Mr. Johnson credits only fourteen per cent of the burrows as being longer than

six feet. He divides the remaining burrows into two classes, one group about two feet long, the other group about four feet in length. In the writer's opinion the latter two classes may to all intents and purposes be regarded as representing the same thing; simply refuges or places for temporary shelter. Mr. Johnson's observations likewise indicate at least a fundamental similarity between the conditions of construction existing in the region he refers to (Illinois) and the conditions to be found in Iowa.

Before closing the introduction it seems fitting to make some mention of the manner in which these animals dig. G. E. Johnson (*ibid.*, p. 266) reports the keeping of a number of these animals in captivity and the observance of their digging habits. He is quoted in part as follows: "In digging, the ground squirrel makes a few, quick, alternating strokes with its fore legs throwing the sand about its hind legs. This is followed by a straightening of the body and quick alternating strokes by the hind legs which throw the soil back with great force, at the same time scattering it."

The writer has observed much the same process in the field, especially during the breeding season when the old males were roaming about constructing new retreats. In some cases the dirt seems to be scattered away from the hole, at least in part, but in many instances no apparent attempt is made to conceal the opening. The writer is of the opinion that the spermophiles do not try to hide their excavations, and that the dirt at the mouth of a hole is only scattered when it accumulates in such quantity that it interferes with the activities of the animal. Holes are eventually rendered inconspicuous by the washing away of loose dirt and regrowth of the sod. The fact that the animals habitually dig their burrows in exposed places, when in many cases locations under bushes or at the edges of hayfields and weed patches present themselves, argues against any very strong instinctive tendency to conceal the burrows.

As previously intimated, the concrete discussion of the subject will be divided into separate considerations of the temporary and the permanent burrows. As the separation into these two groups is based principally on length, no sharp line can be drawn between the two classes and the division is more or less artificial. Its use is justified, however, for it has enabled the writer to bring out the correlation of the animals' life habits and the types of burrows that are utilized. Specific cases and diagrams are included in the fol-

lowing pages, the examples being selected primarily to show diversity of structure. Habits which are closely dependent on burrow structure are necessarily included although they come more properly within the field of general habits. In order to treat the subject as coherently as possible the insects found in the different burrows are simply listed in this chapter as they form the subject matter for a later discussion.

TEMPORARY BURROWS

The structures which may be regarded as temporary burrows or retreats are usually short and of simple construction. For all practical purposes the length may be used to indicate the nature of any particular burrow.

The great majority of the burrows fall into this class. It is likely that even the permanent nesting burrows are at first shallow retreats, a few being dug out and developed because of natural advantages, while the most of the retreats are of only passing value dependent upon circumstances, and eventually fall into disuse.

In any pasture inhabited by the Thirteen-lined *Spermophile* a careful examination and some excavation will reveal the fact that there are many short burrows within a few yards of what are known to be old established dens. Further observation will show that most of these short tunnels or pockets (for they are often merely passage-ways under stumps, which require little effort on the animal's part in construction) are not developed during the summer but are used casually, nevertheless, by the inhabitants of the region. This condition varies in degree, and is dependent largely on the extent to which the animals are persecuted by natural enemies. For these short pockets are used principally as refuges into which the animals retire to eat the various food materials which they obtain above ground. Usually the walls of the tunnel, especially near the entrance, will show the presence of small bits of clover, grass or insect remains. The *spermophiles* increase their feeding territory and yet insure themselves against surprise attacks by constructing a number of these small refuges.

If stumps are present in the infested pasture, many holes will be found about their roots. Tunnels from the holes usually lead directly beneath the stumps, where natural cavities formed by decay are taken advantage of. There may be one or more than one opening, often there are two, and more rarely three. The openings

may be at the very edge of the stump or occasionally a foot or more away. Plate I, fig. 1, shows an example of this type.

A tunnel passes around the stump to join two holes on opposite sides. Often there is a natural central cavity beneath the stump, due to decay, and accessible from the tunnel at various points.

Plate I, fig. 2, shows a temporary retreat that was located in a pasture region among several permanent burrows. This little burrow measured some three and a half feet in total length and was not more than ten inches deep at any point. At the time of investigation both openings were plugged. This is often found to be the case when the burrow is not in use and no explanation can be given in most instances.

Occasionally these retreats under stumps are developed in an interesting and peculiar manner. As the stump decays it gradually falls apart or becomes overturned or otherwise broken away from the roots. This leaves the former retreat exposed or partially so at least. In hard soils, clays particularly, the roots will become partially pulverized while the soil is so dry and hard that it will not immediately fill the cavities caused by the decay. The spermophiles take advantage of this fact, and the writer has excavated many passages which occupied the spaces formerly filled by roots. In fact, the old bark was often found lining the walls. For the bark is thin and resistant and does not decay until the internal portion of the root has long been gone.

Plate I, fig. 3, is a diagram of a short burrow with two openings. It is included because the distal part of the burrow occupied the former position of a branching root which was mainly decayed away.

The writer was at a loss for some time in trying to account for some long burrows which took a fairly straight course and yet ended blindly after gradually becoming smaller in diameter up to the point that they would not permit the passage of a spermophile. Johnson (1917, p. 268) reports the discovery of some long tunnels that ended blindly and suggests that they might function as drains. No mention was made of any tapering in size so these burrows may not have been similar to those mentioned above. It is the opinion of the writer, however, that most of these cases can be explained by the fact that the passages occupy the positions of former roots.

It is difficult to say to just what extent the spermophiles utilize

old root passages. Probably they remove bits of decaying wood and otherwise hollow out the tunnels so formed to suit their conveniences. Burrows of this nature are, however, temporary retreats only. They are longer than the ordinary retreats because their construction is not dependent on the spermophile's efforts alone. Some of these longer retreats are no doubt remodeled eventually to become permanent nesting burrows as they are typically found in the hard soil of pastures where this species prefers to construct its more permanent homes. But in such case the constant use of the passages obliterates all traces of former relations with regard to the roots. Hence this feature is usually noticeable only in the temporary burrows.

An example of a temporary burrow which occupied the former position of a root is shown in the drawing on Plate II, fig. 1. This burrow had been in active use the entire summer until a few days before the time the excavation was made. (September 8). A short period of cold weather had put a stop to activities on the part of the spermophiles and the burrow was abandoned. It was located in an upland pasture, bare stump land for the most part.

The burrow had been plugged with loose dirt for a distance of a foot or more from the mouth. In one pocket about three feet from the external opening, a toad was found which had evidently selected this location in which to hibernate. The burrow followed the course of a decayed root. In fact, there were three holes near the one diagrammed, with burrows radiating from the location of a former stump. The walls of the passageway were lined with old bark and in some cases it was possible to remove whole cylinders of the latter without breaking it. As would be expected the tunnel became progressively smaller toward the distal end, and it was obvious that this portion was not used to any extent.

A somewhat different situation is shown in Plate II, fig. 2. This burrow was observed to be in use the year preceding its excavation, but had evidently not been used as a nesting burrow. At the time of excavation (August 14, 1922) there was much dirt in the passage from B to C and it was evident that the burrow was being lengthened. As in the previous case this burrow followed the course of a decayed root. There were two openings (A and B). The burrow was located in an upland pasture.

Cory (1912, p. 141) quotes Kennicott as saying that in Illinois the males leave the females during the season when the young are

produced and wander about digging temporary burrows or living in some abandoned ones for a few days at a time. He says that some of these burrows are as much as twenty feet in length and contain nests placed in side chambers.

The writer is inclined to believe that these longer burrows were not constructed for strictly temporary use but has noticed their presence if a summer retreat was well situated with reference to the food supply and was used quite regularly accordingly. However, this wandering habits of the males no doubt accounts for many of the short, abandoned and sometimes isolated burrows.

G. E. Johnson (1917, p. 264) mentions the discovery of short burrows in Illinois and says that they are evidently refuges used in journeys between a food source and permanent burrows some distance away. In the same article Johnson mentions that short burrows were found associated with deeper burrows in pastures.

But by no means all of the temporary shelters are of the same nature and location as the foregoing. The spermophiles move about locally with reference to the food supply. Their fondness for grasshoppers leads them into newly cut fields. Here they will remain until the conditions which facilitate the securing of food are no longer operating.

So we find many short retreats scattered over the hay and grain fields in the late summer. They are constructed in the rather loose soil and are very temporary, being obliterated during the winter or by plowing in the spring. Some of these burrows command a more favorable location, being preserved by the proximity of a fence or some other obstacle. In such cases they may even become permanent eventually, especially if they are near a pasture. For this sort of location is admirably suited to the animals' needs as they can feed on the short pasture during the summer and retreat into the holes in the grass of a neighboring field when threatened by natural enemies. Similarly, under such conditions many of their movements are concealed from other animals that prey upon them.

PERMANENT BURROWS

From the exterior there is no apparent difference between a permanent burrow and one of a temporary nature. The only indication of a permanent structure may be the fact that several holes are in close proximity, for there are almost invariably two openings to the old established burrows. Then, too, they are usually situ-

ated in hard soil, pastures being favored, for it is necessary to have the permanent home in ground that is not plowed constantly and is firm enough to prevent collapse of the passages from rains or freezing and thawing.

Plate III represents an upland pasture burrow which was at least three years old and perhaps much older. It was located on a hillside in hard, dry, well drained soil. The passages themselves indicated considerable age, being rather wider than the average and showing signs of wear.

Two interesting facts were made clear in the course of excavation. The pocket A, which incidentally marks the deepest point of the burrow, was used only for the dumping of wastes. This was found to be duplicated by similar conditions in previous excavations and in this instance the proof was conclusive. The pocket was over half filled with coprolites, many of them being of recent deposition.

The passageway B is of interest because it was hollowed out within a decayed root which came from the stump E, as indicated by the dotted lines.

No nests were present although this was an old burrow. This is explainable in that old nests are walled in during the summer and especially after the young are capable of caring for themselves. This burrow was excavated August 9, 1922, at which date the young would have left the parental home. Without doubt the enlargement at D marks the former site of a nest, used either for hibernation in winter or for the raising of young. It is notable that this is practically the deepest point in the burrow. The enlargement at C is no doubt due to constant use of the passage at this point. It is habitual with the spermophiles to carry food within the mouth of the burrow, where it can be eaten with more safety.

Plate IV, fig. 1, represents a burrow from the border of a dry creek bed in a pasture area. It was entered from the north where two openings gave access to the exterior. It will be noted that a short passage about four feet from the openings leads to a nest. This nest was of recent construction and in a good state of preservation. The date, July 27, 1923, indicates that this was about the end of the season that the young are in the nests.

The passage continued on nearly two feet from the nest, and was plugged with dirt after turning slightly. Coprolites were found

scattered on the floor of the pocket thus formed, which bears out the testimony of Plate III.

The plug having been removed, the tunnel was found to lead to another rather new nest, which was placed directly beneath a stump, between the spreading and decaying roots. A passage extended to the surface here, while a deeper tunnel continued through beneath the nest. This latter tunnel took a sharp bend to the left and assumed a more or less straight course for over six feet. This was followed by an elbow bend where an old nest was walled in. The materials of the nest were the usual grasses, but they were old and were mixed with bits of oak leaves, indicating that the nest had been there since the preceding fall and may have served as the retreat of a spermophile during the winter months. Some shells that represented corn grains were found mixed with the nest materials, and they too showed signs of considerable age. It is notable again that this nest was at the deepest point of the burrow, being some 28 inches below the surface.

Plate IV, fig 2, gives an example of a rather short shallow burrow that was evidently used as a place to raise young. There was one inhabitant at the time of excavation, a young male about two-thirds grown.

The nest was situated in an oval chamber about six inches in depth. This pocket had been partially filled with dead and fresh grasses mixed with loose dirt. This rude nest was covered with insect remains and bits of wilted clover which no doubt represented food that had been brought to the young. Several grubs were found in or about the nest. This burrow was excavated June 26, 1922. It was located in an upland field and had obviously been constructed the same year. It was of course much shorter than the average pasture burrow.

G. E. Johnson (1917, p. 264) brings out the relative scarcity of the long permanent burrows when he states that only six of nearly eighty burrows which he examined were found to be branched. He likewise states that the animals were observed to construct nests while in captivity, in which they slept when not active. The writer observed the same habit when experimenting with captive spermophiles. It must be remembered, however, that an animal does not necessarily react in a normal way when taken out of its natural environment.

In regard to nest structure the following is quoted from Johnson (*ibid.*, p. 267) :

"It is in the nest also that food is stored as was proved by the presence of grain in the nests of the three ground squirrels referred to, and in practically every nest examined in the field. Oats, wheat, corn, and weed seeds have been frequently found between the excavated space in the ground and the grassy nest that filled it. In the recently occupied burrows this food varied from considerable in the late summer to a small amount in the late autumn. The nests were usually found in the longer and deeper burrows. Of the seventy-eight burrows recorded twenty-two had nests connected with them. Two of these had two nests."

"Some of the nests were found to one side of the burrows, others at the ends of the burrows and still others in the direct course or at an angle of the burrow. . . . This nest was filled entirely full with unshelled oat kernels and a little dry grass. The estimated number of seeds by counting one-sixteenth of them was 23,000 to 24,000."

The writer's own experience with nests was somewhat similar to the above. Possibly there seemed to be less of a tendency to store grain, but this could be accounted for by varying local conditions as to the availability of food. The habit of storing grain is certainly not universal among the spermophiles.

Cory (1912, p. 141) quotes Kennicott as saying that the nests were sometimes as large as a half bushel, the interior being lined with soft material. The writer found no case of a nest this large. The largest were about ten inches in diameter and these were demonstrated to be nests used in rearing the young.

One phase of burrow structure remains to be touched upon; the type of retreat used during hibernation. Some work has been done on this subject previously, the information being collected by accidental discoveries of individuals undergoing hibernation. The testimony is to the general effect that the animals hibernate in nests in the deeper burrows. This is too well established to be questioned.

Interesting exceptions occur however. The writer observed two cases of spermophiles taking over abandoned burrows of larger animals, which were of course deeper and went down below the frost line. But the great majority of the spermophiles hibernate in their own burrows.

GENERAL CONCLUSIONS AND ECONOMIC BEARING

From the standpoint of agriculture the burrows themselves are harmless enough. They may even be of some slight benefit in allowing the rainfall to soak into the ground more completely. On golf links, parade grounds, parks and similar areas the holes may often become a serious nuisance.

If control measures are attempted in any locality, the significance of burrow structure has a direct bearing on the subject. For if poisoned grain, for instance, is to be laid in the burrows, the time to do it is obviously in the early spring when the animals first appear and may be found almost exclusively in pastures or near the deeper burrows. A little observation will show at once where the ground squirrels are to be found at this time. Later on in the summer the problem of extermination is made much more complicated by the scattering out of the individual spermophiles and the occupancy of the many small retreats. But, as will appear later, the necessity for control is the exception rather than the rule. And almost all of the serious damage done by this species is confined to the planting season.

As to the stage of grain and the relations of food to burrows, the subject is developed in a succeeding chapter on food habits. It is, however, of economic importance, and a study of burrow structure is necessary in order to fully understand it.

FOOD HABITS AND ECONOMIC STATUS

FOREWORD

While engaged in a field survey and study of *Citellus tridecemlineatus tridecemlineatus* some one hundred and twelve stomachs were preserved.

The writer found that the best method in preservation was to empty the stomach contents into a small wide-mouthed bottle of 70% alcohol. This was preferable to placing the entire stomach in preservative because when this latter method was employed the alcohol did not penetrate the rather thick stomach wall soon enough to prevent the beginning of decay.

The spermophiles chew their food well before swallowing it and the materials in the stomach are always well broken up even before the digestive juices have acted upon them to any considerable extent. Hence the stomach contents are quick to decay upon the animal's death.

The fact that these stomach contents are so well pulverized has an obvious disadvantage from the standpoint of the investigator, for in almost all cases it is impossible or at least impractical to attempt accurate identification of the insect remains. Occasionally, legs of grasshoppers are swallowed without being completely mutilated. Some larval segments may also remain more or less intact. Hulls of the common grains are sometimes swallowed entire, as are many weed seeds.

But fortunately, on the other hand, *Citellus tridecemlineatus tridecemlineatus* seems to prefer many of the common and well known grains as well as some of the common and conspicuous insects. So the work of identification was not entirely hopeless. It is the opinion of the writer that the results obtained are entirely dependable and quite characteristic of the species.

W. L. Burnett (1914, p. 11) mentions the same difficulties in identifying the stomach contents of *Citellus tridecemlineatus pallidus*. Furthermore he is of the opinion that it is somewhat easier to identify the vegetable materials than to identify the insect remains.

DATA GAINED FROM FORMER INVESTIGATIONS
OF FOOD

C. P. Gillette (1889) examined some twenty-two stomachs of *Citellus tridecemlineatus tridecemlineatus*, the animals being killed between April 19 and August 2. He found that insects made up a large proportion of the food, and further, that the insects eaten were almost exclusively injurious. He stated it as his opinion that this animal was of decided benefit to gardens, lawns, meadows, and pastures. Similarly, he believed that this spermophile would be advantageous to cornfields if it could be prevented from digging up the newly planted grain, for it would destroy large numbers of cutworms before planting time.

J. M. Aldrich (1892) in summing up some examinations of the food of *Citellus tridecemlineatus tridecemlineatus* found that relatively large numbers of cut-worms, grasshoppers and crickets were eaten. Some neutral beetles were also found in the food materials. Aldrich seemed to think that this species was approximately neutral in its economic importance.

W. L. Burnett (1914, p. 10) gives some very interesting data with reference to *Citellus tridecemlineatus pallidus*. He states that a specimen kept in captivity would leave all other foods untouched when grasshoppers were available. The legs and wings of the grasshoppers were not eaten. This specimen would catch, kill, and eat mice as well as grasshoppers, when these animals were placed in its cage.

W. L. Burnett (ibid., p. 11) gives the following list of food materials eaten by *Citellus tridecemlineatus pallidus* where in captivity: sunflower seed, grass seed, dandelion seed, pumpkin seed, sugar beet seed, watermelon seed, muskmelon seed, young chickens, squash seed, speltz, beans, grasshoppers, crickets, beetles, alfalfa roots and leaves, corn, cane, oats, wheat, kaffir corn, rye, milo maize, peas, barley, peanuts and field mice.

Some forty-six stomachs of *Citellus tridecemlineatus pallidus* were examined by Burnett (ibid., p. 15). All of these specimens were taken in northern Colorado during the summers of 1912, 1913 and 1914. He found the stomachs to contain a rather high percentage of animal matter. Remains of grasshoppers, beetles and field mice predominated. Corn, alfalfa, spiders, caterpillars and in one case a bird feather, were found in the various stomachs.

DAMAGE

The principal charge against this species is that it destroys young crops. Corn crops are sometimes damaged to the extent that replanting becomes necessary.

The attacks usually occur along the margins of cornfields which are bordered by meadows. The spermophiles dig down at the base of each newly-sprouted corn stalk and in this manner obtain the planted grain. The young corn dies as a result.

Such depredations are quite common throughout the state of Iowa. Fortunately, however, the damage is so slight that it usually passes unnoticed. It is seldom that the corn is molested beyond the third row from the edge of the field. But occasionally, if the spermophiles are present in large numbers the actual loss to the farmer may be considerable.

A few years ago when this species was somewhat more numerous in individuals, serious losses of young corn were not uncommon. Stoner (1918, p. 32) quotes an early report of Vernon Bailey to the effect that large fields of corn were sometimes destroyed and had to be planted over several times. Even fields of small grain were at times seriously damaged by spermophile invasions in the late eighties of the past century.

But according to all available reports the numbers of spermophiles have been very materially reduced in the last decade. It is perhaps safe to say that there has been a fifty per cent reduction in the preceding five years. Bounties have been offered for this species, and literature has been circulated about the country advising the people as to the different methods used in poisoning rodents.

With this loss in numbers has come corresponding reduction in the amount of damage done. Occasionally one hears accounts of attacks upon corn. The writer has recently investigated some of these claims and has found that they are very generally grossly exaggerated.

As far as attacks on oats, wheat, barley, rye, and similar crops are concerned, the damage is of little consequence. These grains may be attacked just after sprouting. But the destruction is never great enough to necessitate replanting. Occasionally the ripe grain is eaten or stored in the fall, as mentioned in preceding discussions. However, grasshoppers are easily obtainable at this season of the year, and *Citellus tridecemlineatus tridecemlineatus* prefers these insects to any other form of food.

It has been claimed that garden crops are sometimes injured by this species. The writer, however, has been unable to discover any real proof of this. No doubt peas, beans, and similar vegetables are sometimes taken, but certainly not in any considerable quantities. *Spermophiles* kept in captivity would only eat peas, beans, and the seeds of other garden plants when no other foods were available.

There is little or no damage to pasture land because of the presence of burrows. No obstructions, such as piles of loose dirt, are thrown up by this species. Similarly, there is practically no injury to the grass because it almost always grows up to the very edges of the holes.

There is no doubt, however, that the burrows are somewhat of a nuisance to golf links, parade grounds, and similar areas where a smooth unbroken surface is desirable.

BENEFITS DERIVED

At the beginning of this consideration we are confronted by the fact that we cannot hope to determine the identity of many insect remains found in the stomachs of this species. For not only does this animal chew up its food very thoroughly, but it bites off and discards the heads, wings, and legs of the insects in most cases, and these rejected parts are the ones that lend themselves particularly well to identification. But the task is by no means hopeless, and it is possible to make some fairly accurate estimates.

Of the larvæ eaten in the spring it is safe to say that a great many are detrimental to agricultural pursuits. For they are of necessity species that live upon the cultivated crops and grasses. It has previously been determined that cut-worms constitute a regular article of diet at this season.

It is quite true that *Citellus tridecemlineatus tridecemlineatus* exercises little or no choice in the selection of insect food in the spring, probably because the insects are none too numerous at this time. But in the fall when insect life is abundant and diversified a very decided choice is exercised.

Perhaps the strongest argument in favor of the Thirteen-lined *Spermophile* is the fact that it consumes large quantities of grasshoppers in the latter part of the season. It is observable, both in the field and in the cases of animals kept in captivity, that the members of this species seem to prefer grasshoppers to any other food. Grasshopper remains may be identified among the stomach contents because in this case the enlarged proximal portions of the

hind legs are often swallowed entire. The heads, wings, and remaining leg parts are discarded. The appended chart (Plate V), shows what a large proportion of the food matter is made up of grasshoppers, particularly in the late summer and early fall. Some weed seeds are eaten by the Thirteen-lined *Spermophile* at every season of the year. Here, however, there is apparently very little choice in the selection of food, and whatever is most accessible is utilized. Seeds of rag weed, hemp, fox-tail, and pig weed are commonly eaten. But on the other hand clover seed forms a staple article of diet, whenever available. And ordinarily the eating of clover seed would be considered as disadvantageous to agricultural interests. So perhaps the good done in the destruction of weed seeds is counterbalanced by the harm done in consumption of clover seed.

ECONOMIC CONCLUSIONS WITH REGARD TO THE FOOD HABITS

C. P. Gillette (1889) believed that *Citellus tridecemlineatus tridecemlineatus* was advantageous to agricultural pursuits. He examined twenty-two stomachs and based his conclusions on the results of this investigation.

J. M. Aldrich (1892) investigated *Spermophilus tridecemlineatus*, and seemed inclined to consider this form about neutral in economic status. This work was done in the Dakotas, so the species referred to was undoubtedly what is known as *Citellus tridecemlineatus pallidus*.

W. L. Burnett (1914) collected forty-six stomachs of the western subspecies, *Citellus tridecemlineatus pallidus*. As in the case of the present investigation a large proportion of the food was found to consist of insect remains. Burnett probably considered this species to be neutral in its economic importance. It is interesting to note the answers he received to letters of inquiry that were sent out to some of the farmers of northern Colorado. In every case the farmers were quick to notice any depredations, but they failed to recognize that any good might result from the presence of this form. A parallel could be pointed out in the former public attitude toward many of our useful hawks and owls.

Vernon Bailey (1893, p. 42) examined stomach contents of this species and its geographical races. He came to the conclusion that it probably did more harm than good. Harm by virtue of the damage to young crops, and good because of the numbers and kinds

of insects eaten. The writer is inclined to think this was a very fair estimate. But as before intimated, since the numbers of spermophiles have been greatly reduced, the damage to young crops is negligible.

It is even likely that this species will not disturb the corn, if represented by only a moderate number of individuals. For when the spermophiles are not especially numerous, they can obtain enough food in the way of insect larvæ without leaving their natural haunts and invading the cultivated fields.

A glance at the appended chart will show the high percentage of insects eaten by *Citellus tridecemlineatus tridecemlineatus*. Further observations will show that the majority of these insects, taking an average for the season, are grasshoppers. It is safe to say that grasshoppers cause a five per cent annual loss to hay crops alone.

Without doubt, this species acts as an important natural check upon the increase of grasshoppers.

Man's attempts to disturb the balance in nature have quite commonly resulted in disaster from an agricultural standpoint, particularly when he has destroyed some species which acted as a natural check upon a noxious form. We find an example of this in the destruction of the Prairie Chicken and the succeeding increase in the numbers of grasshoppers.

It is the opinion of the writer that unless some very serious charge is brought against a species, it is the part of safety to leave the balance of nature undisturbed, especially in cases like the one under consideration where the animal preys upon an undesirable form.

As intimated in the preceding pages, these spermophiles are not numerous enough in most localities to destroy any great amount of young corn. Should they become too populous in a given area it is a simple matter to reduce their numbers practically overnight. Some effective means of eliminating these animals will be found in the following chapter. In conclusion, we may even admit that with the exception of grasshoppers, no discrimination is exercised in the choice of insect foods. Perhaps equal numbers of beneficial and harmful insects are destroyed. But in any event, if the damage to young corn is not serious, it is most emphatically desirable to retain this species as a check upon grasshoppers. For even a one per cent increase in the numbers of grasshoppers would mean a very large total loss to cultivated crops each year.

So as long as this species exists in moderate numbers it may be

regarded as a desirable element in the fauna of a given region. Certainly active measures to secure its elimination should not be necessary.

ANALYSIS OF STOMACH CONTENTS

In the following pages analyses of the materials found in eighty-two stomachs will be found. As previously stated, one hundred and twelve stomachs were collected in 1922 and 1923. All of these were examined, but a number of them proved to be empty. The latter have not been included in this appendix because they have no particular significance. They merely represented individuals killed in the early part of the day, probably before any food had been eaten.

Stomach No. 1—female; Iowa City, Iowa; May 14, 1922.

- 85% insect larvæ.
- 10% blue grass and white clover tips.
- 5% weed seeds.

Stomach No. 2—female; Iowa City, Iowa; May 14, 1922.

- 60% insect larvæ.
- 30% blue grass and white clover.
- 7% weed seeds.
- 3% unidentified vegetable materials.

Stomach No. 3—male; Iowa City, Iowa; May 14, 1922.

- 80% insect larvæ, at least one-half of them cutworms.
- 20% vegetable matter. Chiefly grass and white clover.

Stomach No. 4—male; Iowa City, Iowa; May 16, 1922.

- 20% insect larvæ.
- 40% corn.
- 25% grass and white clover.
- 5% various weed seeds.
- 10% unidentified vegetable materials.

Stomach No. 5—male; Williamsburg, Iowa; May 20, 1922.

- 40% insect remains. Evidently all larvæ.
- 40% corn.
- 20% grass, clover, and unidentified vegetable matter.

Stomach No. 6—female; Victor, Iowa; May 21, 1922.

- 45% insect remains.
- 20% corn.
- 20% clover and grass.
- 5% weed seeds.
- 10% unidentified vegetable materials.

Stomach No. 7—female; Victor, Iowa; May 21, 1922.

Stomach nearly empty. Some signs of insect remains.

Stomach No. 8—male; Victor, Iowa; May 21, 1922.

- 30% insect remains.
- 60% white clover.

- 10% unidentified vegetable materials.
- Stomach No. 9—female; Iowa City, Iowa; May 28, 1922.
- 20% white clover.
- 10% various weed seeds.
- 60% corn.
- 10% unidentified materials.
- Stomach No. 10—male; Iowa City, Iowa; May 28, 1922.
- 40% white clover seed.
- 20% various weed seeds.
- 20% grass and clover.
- 20% unidentified matter.
- Stomach No. 11—female; Iowa City, Iowa; May 28, 1922.
- 40% insect remains.
- 30% wheat.
- 15% blue grass and white clover.
- 15% unidentified.
- Stomach No. 12—female; Iowa City, Iowa; May 28, 1922.
- This stomach was practically empty. A few corn hulls were found.
- Stomach No. 13—male; Iowa City, Iowa; May 29, 1922.
- 20% insect matter.
- 30% wheat.
- 40% grass and white clover.
- 10% unidentified.
- Stomach No. 14—female; Iowa City, Iowa; June 2, 1922.
- This specimen filled with the remains of a field mouse.
- Stomach No. 15—female; Iowa City, Iowa; June 2, 1922.
- 30% insect remains.
- 10% corn.
- 20% white clover seed.
- 40% grass and clover.
- Stomach No. 16—male; Iowa City, Iowa; June 3, 1922.
- 30% insect remains.
- 20% corn.
- 50% blue grass and clover.
- Stomach No. 17—male; North Liberty, Iowa; June 4, 1922.
- 35% insect larvæ.
- 25% corn.
- 40% blue grass and clover.
- Stomach No. 18—female; North Liberty, Iowa; June 4, 1922.
- 40% insect matter.
- 55% grass.
- 5% weed seed.
- Stomach No. 19—female; Eagle Grove, Iowa; June 10, 1922.
- 40% insect larvæ.
- 40% grasses.
- 10% weed seed.
- 10% unidentified.

Stomach No. 20—male; Iowa City, Iowa; June 29, 1922.

60% remains of a field mouse.

30% insect larvæ.

10% grass, clover, and clover seed.

Stomach No. 21—female; Iowa City, Iowa; June 29, 1922.

60% white clover seed.

30% blue grass and white clover.

10% unidentified.

Stomach No. 22—female; Iowa City, Iowa; June 30, 1922.

70% white clover seed.

20% white clover tops.

10% grasses.

Stomach No. 23—female; Iowa City, Iowa; June 30, 1922.

30% insects.

40% white clover seed.

30% grass and white clover tops.

Stomach No. 24—male; North Liberty, Iowa; July 3, 1922.

Contained two young meadow mice.

Stomach No. 25—female; North Liberty, Iowa; July 3, 1922.

35% insect matter.

10% white clover seed.

50% blue grass and clover.

5% unidentified.

Stomach No. 26—male; North Liberty, Iowa; July 3, 1922.

Practically empty. A few white clover seeds were found.

Stomach No. 27—male; Iowa City, Iowa; July 7, 1922.

60% unidentified insect materials.

30% grasshoppers.

10% blue grass, white clover, and white clover seed.

Stomach No. 28—male; Midriver, Iowa; July 10, 1922.

10% grasshoppers.

20% other insects.

30% white clover seed.

30% white clover and blue grass.

10% unidentified.

Stomach No. 29—female; Midriver, Iowa; July 10, 1922.

90% blue grass.

10% white clover seed and some weed seed.

Stomach No. 30—female; Midriver, Iowa; July 10, 1922.

75% blue grass.

10% white clover seed.

15% weed seeds.

Stomach No. 31—male; Iowa City, Iowa; July 24, 1922.

20% grasshoppers.

30% white clover seed.

10% various seeds.

30% blue grass.

10% unidentified (some insect remains).

- Stomach No. 32—male; Iowa City, Iowa; July 24, 1922.
10% grasshoppers.
20% unidentified insects.
20% various weed seeds.
10% oats.
40% blue grass.
- Stomach No. 33—male; Iowa City, Iowa; August 6, 1922.
95% grasshoppers.
5% unidentified materials.
- Stomach No. 34—female; Iowa City, Iowa; August 6, 1922.
Entirely filled with grasshoppers.
- Stomach No. 35—male; Victor, Iowa; August 7, 1922.
90% grasshoppers.
10% grass and unidentified materials.
- Stomach No. 36—male; Victor, Iowa; August 7, 1922.
90% grass and white clover.
5% white clover seed.
5% unidentified.
- Stomach No. 37—male; Victor, Iowa; August 7, 1922.
Contained one small field mouse.
- Stomach No. 38—female; Iowa City, Iowa; August 16, 1922.
Entirely filled with grasshoppers.
- Stomach No. 39—female; Iowa City, Iowa; August 16, 1922.
60% grasshoppers.
40% grass and clover leaves.
- Stomach No. 40—male; North Liberty, Iowa; August 17, 1922.
Entirely filled with grasshoppers.
- Stomach No. 41—female; North Liberty, Iowa; August 17, 1922.
Entirely filled with grasshoppers.
- Stomach No. 42—male; North Liberty, Iowa; August 17, 1922.
10% grasshoppers.
90% young oats.
- Stomach No. 43—male; North Liberty, Iowa; August 17, 1922.
Practically empty. Some traces of grass were found.
- Stomach No. 44—male; Iowa City, Iowa; August 18, 1922.
90% grasshoppers.
10% white clover.
- Stomach No. 45—female; Iowa City, Iowa; August 18, 1922.
Almost empty. A few grasshopper remnants.
- Stomach No. 46—male; Iowa City, Iowa; August 19, 1922.
60% grasshoppers.
40% grass and clover.
- Stomach No. 47—male; Lake Okoboji, Iowa; September 4, 1922.
40% grasshoppers.
20% other insects.
30% corn.
10% weed seed.

- Stomach No. 48—male; Lake Okoboji, Iowa; September 4, 1922.
60% grasshoppers.
40% grass and clover.
- Stomach No. 49—female; Lake Okoboji, Iowa; September 4, 1922.
Practically full of new corn.
- Stomach No. 50—male; Lake Okoboji, Iowa; September 4, 1922.
60% grasshoppers.
40% new corn.
- Stomach No. 51—female; Lake Okoboji, Iowa; September 4, 1922.
Full of new corn.
- Stomach No. 52—female; Lake Okoboji, Iowa; September 8, 1922.
30% grasshoppers.
60% corn.
10% unidentified.
- Stomach No. 53—male; Lake Okoboji, Iowa; September 8, 1922.
Practically full of grasshoppers.
- Stomach No. 54—female; Lake Okoboji, Iowa; September 8, 1922.
Practically full of grasshoppers.
- Stomach No. 55—male; Milford, Iowa; September 10, 1922.
90% grasshoppers.
10% corn.
- Stomach No. 56—male; Spencer, Iowa; September 10, 1922.
A few grasshoppers.
- Stomach No. 57—male; Iowa City, Iowa; May 14, 1923.
About a quarter full of oats.
- Stomach No. 58—female; Iowa City, Iowa; May 14, 1923.
A few hulls of corn were found in this specimen.
- Stomach No. 59—female; Iowa City, Iowa; May 15, 1923.
60% insect larvæ.
40% grass.
- Stomach No. 60—male; Iowa City, Iowa; May 16, 1923.
90% grass.
10% weed seeds.
- Stomach No. 61—male; West Branch, Iowa; May 20, 1923.
10% insect remains.
80% weed seeds.
10% unidentified.
- Stomach No. 62—female; Iowa City, Iowa; June 10, 1923.
10% insect remains.
40% white clover stems.
50% weed seeds.
- Stomach No. 63—male; Iowa City, Iowa; June 10, 1923.
90% grass and white clover.
10% weed seeds.
- Stomach No. 64—male; Millersburg, Iowa; June 12, 1923.
Half full of unidentifiable insect remains.
- Stomach No. 65—female; Millersburg, Iowa; June 12, 1923.
Half full of insect remains.

Stomach No. 66—male; Columbus Junction, Iowa; June 20, 1923.

40% insect remains.

10% grass.

30% weed seeds.

Stomach No. 67—female; Iowa City, Iowa; June 26, 1923.

70% unidentified insect matter.

20% grass.

10% clover seed.

Stomach No. 68—male; Iowa City, Iowa; June 29, 1923.

20% unidentified insects.

10% grasshoppers.

40% grass and clover.

30% white clover seed.

Stomach No. 69—male; Iowa City, Iowa; June 29, 1923.

20% insects.

60% grass.

20% white clover seed.

Stomach No. 70—female; Midriver, Iowa; July 3, 1923.

Half full of white clover seed.

Stomach No. 71—female; Midriver, Iowa; July 3, 1923.

10% insects.

90% white clover seed.

Stomach No. 72—male; Marengo, Iowa; July 12, 1923.

40% grasshoppers.

40% grass.

20% clover seed.

Stomach No. 73—male; Marengo, Iowa; July 12, 1923.

A few grasshopper remnants.

Stomach No. 74—female; Iowa City, Iowa; July 30, 1923.

90% grasshoppers.

5% grass and clover.

5% unidentified.

Stomach No. 75—male; Iowa City, Iowa; August 2, 1923.

60% grasshoppers.

30% seeds, (mainly white clover).

10% unidentified material.

Stomach No. 76—male; Iowa City, Iowa; August, 1923.

60% grasshoppers.

20% new corn.

20% clover seed.

Stomach No. 77—male; Iowa City, Iowa; August 9, 1923.

20% unidentified insects.

80% grass and white clover stems.

Stomach No. 78—female; Brooklyn, Iowa; August 10, 1923.

Half full of small grasshoppers.

Stomach No. 79—male; Brooklyn, Iowa; August 10, 1923.

A few grasshopper remains.

Stomach No. 80—male; Colfax, Iowa; August 11, 1923.

30% grasshoppers.

70% oats.

Stomach No. 81—female; Iowa City, Iowa; September 2, 1923.

70% grasshoppers.

30% grass and white clover.

Stomach No. 82—female; Iowa City, Iowa; September 2, 1923.

A few grasshopper remains.

NATURAL ENEMIES AND ARTIFICIAL CONTROL

NATURAL ENEMIES

As natural enemies of *Citellus tridecemlineatus tridecemlineatus* some of the common hawks should receive special mention. The writer observed one instance where a Cooper's Hawk practically exterminated the ground squirrels of an upland pasture. The Red-tailed Hawk and its varieties are persistent enemies of the spermophile. Sharp-shinned Hawks, Marsh Hawks and Sparrow Hawks have been seen to attack this species.

The domestic cat should probably rank second as an agency in control. Certain cats seem to acquire a special liking for ground squirrels and become exceedingly adept at catching them.

Snakes kill considerable numbers of spermophiles. Bull snakes, blue-racers, hog-nosed snakes and occasionally garter snakes figure in this capacity.

Weasels and the smaller mink are effective enemies of the ground squirrel. Although they hunt principally at night, their slender forms permit them to enter many of the spermophile burrows with ease. There is no doubt that many ground squirrels meet death through these night attacks.

Wolves, foxes and eagles destroy ground squirrels, but in Iowa, at least, these animals are not present in sufficient numbers to serve as potent controlling factors.

Perhaps skunks and owls should be mentioned. But all of the species belonging to these groups are inclined to be nocturnal or crepuscular and do not come in contact with the strictly diurnal spermophiles very frequently.

External parasites are rather uncommon on *Citellus tridecemlineatus tridecemlineatus*. All of the individuals killed or trapped were carefully examined and in only a few cases were any parasites found. All of these were discovered during the latter part of April or early in May, just after the animals came out of hibernation. No parasites were found after May fifteenth, indicating that the spermophiles are able to dispose of the pests when they resume active life.

Over half of the parasites found were fleas. All of them be-

longed to the family *Pulicidae*. F. C. Bishopp (1915, p. 12) enumerates the fleas found on American ground squirrels as follows:

The Indian rat flea—*Xenopsylla cheopis* Roth.

The European rat flea—*Ceratophyllus fasciatus* Bosc.

The human flea—*Pulex irritans* L.

The European mouse flea—*Leptopsylla musculi* Duges.

The dog flea—*Ctenocephalus canis* Curtis.

The squirrel fleas—*Hoplopsyllus anomalus* Baker and *Ceratophyllus acutus* Baker.

The cat flea—*Ctenocephalus felis* Bouche.

All of these fleas are parasitic on rats and other animals, including man. Some are known to carry the bubonic plague if there is a source of infection. The California ground squirrel (*Citellus beecheyi beecheyi*) was discovered as an agent in the transmissal of this disease, through the medium of parasitic fleas. (Lantz, 1921, pp. 12-13). It has been found necessary in the interests of human health to destroy large numbers of California Ground Squirrels over infected areas.

It is not beyond possibility that *Citellus tridecemlineatus tridecemlineatus* might aid indirectly in the spreading of similar infections, either now or in the future. But the inconsiderable numbers of parasites found on this species precludes the possibility that it will ever be a dangerous factor in human environment. At any rate, the same potential possibility occurs among man's domestic animals, whose infection-carrying parasites are legion compared with those of the spermophile.

In one case a mosquito was found upon the body of a Thirteen-lined Spermophile. Two small flies were likewise found.

Several arachnids belonging to the family *Ixodidae* were found clinging to the spermophiles. These ticks were the only parasites of importance noted, excepting of course, the fleas. Ticks, like fleas, are concerned in transmitting a parasite from the blood of one animal to that of another. A tick-borne parasite is *Piroplasma bigeminum*, responsible for the stock disease known as Texas fever. The ticks found on the spermophiles of the upper Mississippi Valley are probably non-injurious in this connection, although the potential possibility of spreading disease exists.

CONTROL MEASURES

When Thirteen-lined Spermophiles become so thick in a given locality as to actually menace young crops, active control measures are of course desirable.

The damage is only noticeable in the spring and this is the most opportune time to apply the remedy, for in the spring the range of the spermophile is more restricted than later in the season, and killing the adults at this time forestalls reproduction.

The use of poisoned baits is a quick and efficient method for destroying these animals. The baits should always be placed in the entrances of the burrows. Otherwise they would undoubtedly be eaten by useful species, both wild and domestic.

D. E. Lantz (1921, p. 15) gives the following formula for poisoning the smaller ground squirrels: "Mix 1 tablespoonful of laundry starch in $\frac{1}{2}$ teacup of cold water, and stir it into $\frac{1}{2}$ pint of boiling water to make a thin clear mucilage. Mix 1 ounce of powdered strychnine with 1 ounce of powdered bicarbonate of soda, and stir the mixture into the hot starch, making a smooth, creamy paste free from lumps. Stir in $\frac{1}{4}$ pint of heavy corn syrup and 1 tablespoonful of glycerin, and finally, 1 scant teaspoonful of saccharin. Apply to 20 quarts of oats, and mix thoroughly to coat every kernel. Each quart of the poisoned grain should make forty to sixty baits."

A similar formula is given by W. L. Burnett (1914, p. 15):

Whole corn	16 quarts
Powdered strychnine	1 ounce
Saccharine	1 teaspoonful
Flour	$\frac{3}{4}$ pint
Salt	1 quart
Water	1 quart

As in the preceding case, the poison mixture is poured over the grain. Burnett's experiments showed that one or two poisoned kernels would kill a spermophile.

A slightly different but very effective method of exterminating the animals is carbon bisulphid, poured on balls of cotton, which are then pushed down the mouth of the burrow. The openings of the burrow are then closed. The carbon bisulphid will evaporate rapidly, and the spermophiles will be killed by the poisonous fumes. This method has the advantage that there is no chance of poisoning other animals unintentionally through its practice. It must be remembered that carbon disulphid is a highly explosive liquid and should not be handled near a fire or by an individual who is smoking.

Often considerable numbers of spermophiles may be killed by shooting them with a small-bore rifle. This requires accurate shoot-

ing and considerable effort and patience on the part of the hunter. Unless the ground squirrels are shot through the head or thorax they will crawl into their holes to die a lingering death.

Trapping is a still more unsatisfactory method. A number 0 or number 1 steel trap may be used to catch this species. Simply hollow out a cavity at the mouth of the burrow for the trap to rest in, and cover the set lightly with dirt. This means of extermination is not recommended because so many spermophiles escape after having their feet cut off.

On the whole, poisoning is much to be preferred. It is simple, fairly safe, and does not require as much time and effort as the other methods. Besides, the results are immediate and pronounced.

BIBLIOGRAPHY

- Aldrich, J. M., Food Habits of the Striped Gopher, So. Dak. Agr. Coll. and Exp. Sta., Bull. No. 30, 1892.
- Audubon, J. J., and Bachman, J., The Quadrupeds of North America, Vol. I, 1894, 177.
- Bailey, Vernon, Article on *Spermophilus tridecemlineatus*, Ann. Rept. U. S. Dept. Agr., 1887, 437.
- Bailey, Vernon, Article on *Spermophilus tridecemlineatus*, U. S. Dept. Agr., Bull. No. 4, 1893, 43.
- Baird, S. F., Mammals of North America, 1859, 316-319.
- Bell, Wm. B., and Piper, S. E., Extermination of Ground Squirrels, Gophers, and Prairie Dogs in North Dakota, No. Dak. Agr. Sta. Circ., 4, 1915.
- Bishopp, F. C., Fleas, U. S. Dept. Agr., Bull. No. 248, 1915, 11-15.
- Burnett, W. L., The Striped Ground Squirrels of Colorado, Office State Entomologist, Circ. 14, 1914.
- Cory, C. B., Mammals of Illinois and Wisconsin, Field Mus. Nat. Hist. Zool. Ser., Vol. XI, 1912, 138.
- Coues, E., and Allen, J. A., Monograph of North American Rodentia, Rept. U. S. Geol. Surv., Vol. XI, 1887, 871.
- Elliott, D. G., A Synopsis of the Mammals of North America and the Adjacent Seas, Field Columbian Mus. Zool. Ser., Vol. II, 1901, 100.
- Elliott, D. G., A Checklist of the Mammals of the North American Continent, the West Indies and the Neighboring Seas, Field Columbian Mus. Pub. 105, 1905, 104.
- Flower, W. H., and Lydekker, R., An Introduction to the Study of Mammals Living and Extinct, 1891, 156.
- Gillette, C. P., Food Habits of the Striped Prairie Squirrel, Ia. Agr. Exp. Sta., Bull. No. 6, 1889.
- Goodrich, S. A., Illustrated History of the Animal Kingdom, 1859, 364.
- Herrick, C. L., The Mammals of Minnesota, Geol. and Nat. Hist. Surv. Minn., Bull. No. 7, 1892, 165.
- Hornaday, W. T., The American Natural History, 1904, 94.
- Hornaday, W. T., The American Natural History, Vol. I, 1914, 197.
- Hoy, P. R., Hibernation of *Spermophilus tridecemlineatus*, Proc. Amer. Assoc. Adv. Sci., Aug. 1875, 148.
- Johnson, G. E., The Habits of the Thirteen-lined Ground Squirrel, Quart. Journ. Univ. of No. Dak., Vol. VII, No. 3, Apr. 1917, 261.
- Kingsley, J. S., The Standard Natural History, Vol. V, 1886, 125.
- Lantz, D. E., Rodent Pests on the Farm, Farmers Bull. 932, U. S. Dept. Agr., 1921, 11.
- Lee, T. G., Implantation of the Ovum in *Spermophilus tridecemlineatus*, Mark Anniversary Volume, Science, 1902, 417.

- Lee, T. G., On the Early Development of *Spermophilus tridecemlineatus*, a New Type of Mammalian Placentation, Science, N. Ser., Vol. XV, No. 379, 1902a, 525.
- Richardson, J., (Swainson and Kirby), Fauna Boreali Americana or The Zoology of the Northern Parts of British America, 1892, 177.
- Seton, E. T., *Citellus tridecemlineatus*, Life Histories of Northern Animals, Vol. I, 394.
- Stone, W., and Cram, W. E., American Animals, 1905, 161.
- Stoner, Dayton, The Rodents of Iowa, Ia. Geol. Surv. Bull. No. 5, 1918, 29.
- Tenney, Sanborn, A Manual of Zoology, 1882, 91.
- U. S. Department of Agriculture, Directions for Poisoning Ground Squirrels, Form Bi-176, 1918.
- Warren, E. R., The Mammals of Colorado, 1910, 159.
- Wood, F. E., Mammals of Champaign County, Illinois, Bull. Ill. St. Lab. Nat. Hist., May, 1910, 524.

PLATE I

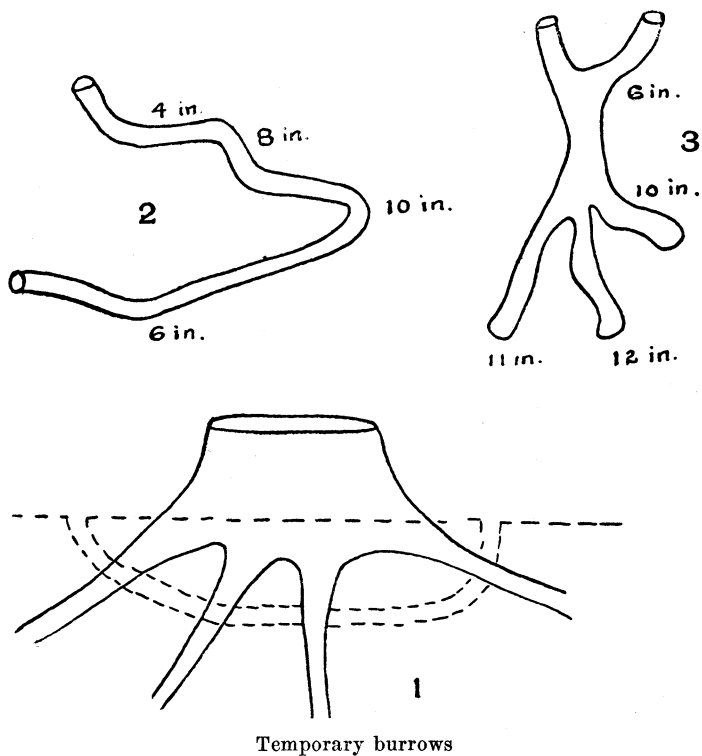
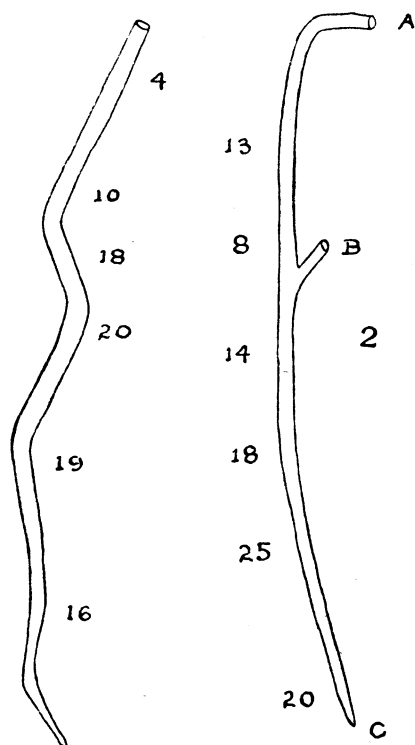
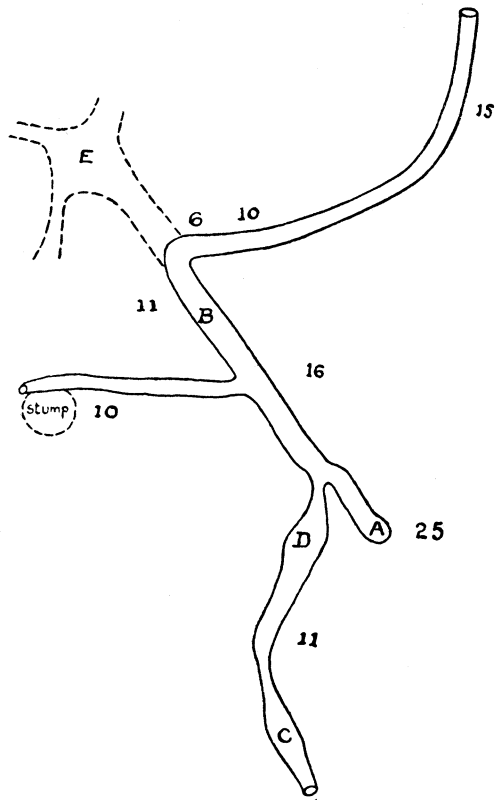


PLATE II



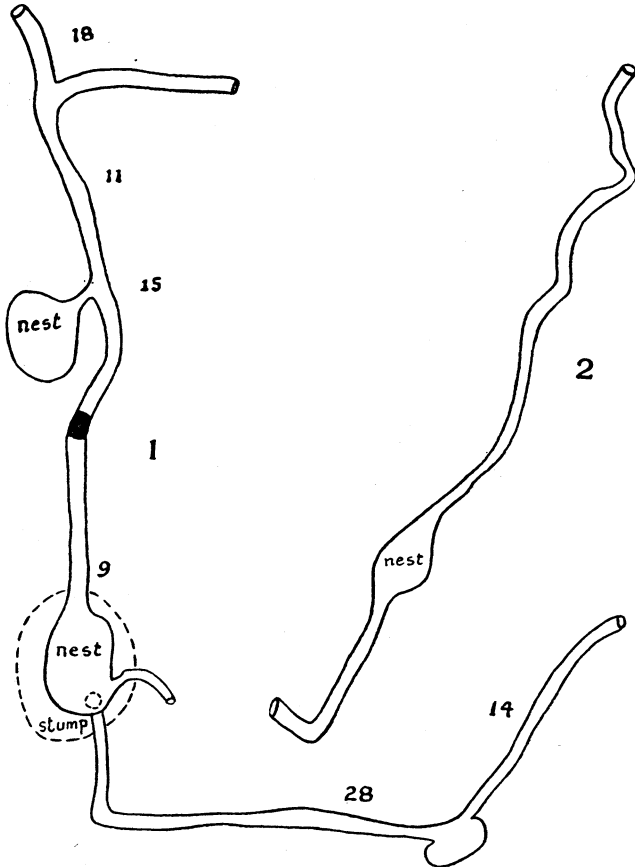
Temporary burrows

PLATE III



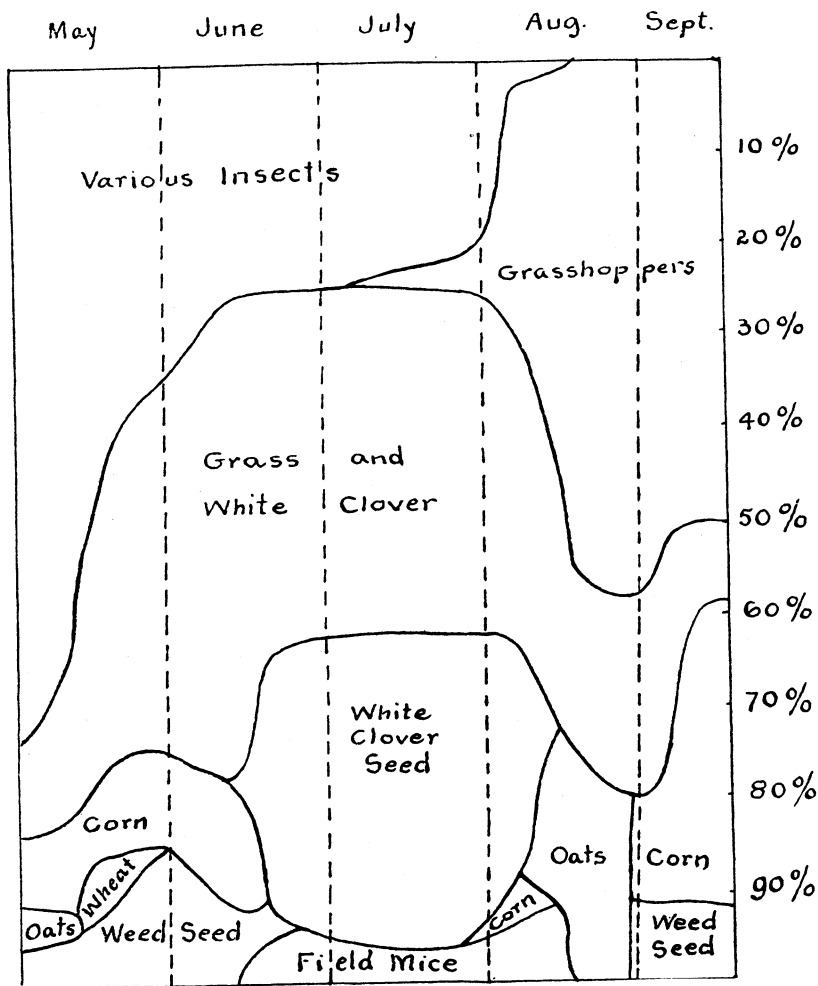
Permanent burrow

PLATE IV



Permanent burrows

PLATE V



Food chart

UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

VOLUME XI

NUMBER 2

THE LIFE HISTORY AND BIONOMICS OF APHIS RUMICIS

by

JOHN LOUIS HORSFALL

PUBLISHED BY THE UNIVERSITY, IOWA CITY

Iowa Univ. Lib.
24
8-17-1925

INTRODUCTION

The identity of *Aphis rumicis* Linn. has been of interest to aphidologists in various countries for many years. The early practice of naming species of aphids from the host plants upon which they commonly occurred, while of value to a large extent in aiding in the future recognition of the species, resulted in some cases in the making of synonyms. With the advent of careful life history studies and the recognition of the fact that aphids may select plants widely removed botanically from their summer hosts upon which to hibernate, the synonymy of many aphids has been worked out with more certainty. In the case of *Aphis rumicis* Linn., we find that forms occurring on different host plants were described as separate species when, in many instances, the only differentiating character given by the author was the general body color, a character which is of little specific value, in the tribe Aphidini as a whole, in separating closely related species.

I have pursued detailed studies on the biology of this species during four seasons and from these data have secured definite evidence on the identity of forms occurring on widely dissociated species of host plants at different periods during the year. Although the number of food plants reported for *Aphis rumicis* is extremely large, nine additional species are given in these studies. Detailed life history studies and generation experiments are reported for the first time. Among the records of natural enemies will be found the names of several interesting forms not, as yet, connected with *Aphis rumicis* in literature. My own material has been collected in Iowa and Eastern Pennsylvania. The English material was obtained through the courtesy of Professor F. V. Theobald, and the California specimens, representing collections of Swain and Davidson, were kindly loaned by Professor G. F. Ferris of Stanford University. I wish to express my appreciation to Professor H. F. Wickham, State University of Iowa, for his valuable criticism in the preparation of these studies, to Dr. A. C. Baker, Bureau of Entomology, United States Department of Agriculture, for his suggestions while I was examining material in the collection of the Bureau and the notes of Dr. Asa Fitch and

Mr. Theo. Pergande, and to Messrs. A. B. Gahan and H. E. Ewing of the United States National Museum for their determinations of parasitic material.

PREVIOUS WORK ON THE PROBLEM

For a century and a half after publication of the original description of *Aphis rumicis* by Linnæus, all printed references related to its occurrence in different localities on various host plants with occasional descriptions of the summer forms. The first record of biological observations on the species, which has come to my attention, was published by Walker (97) who noted the fact that this aphid hibernated on the common furze. Buckton (2) made transfers from foxglove to common broom with negative results.

Biological observations of a detailed nature were published by Theobald (88), in 1912, and were based on collections and notes from England and on other European material. He outlined two cycles: one starting with ova and fundatrices on *Euonymus europæus* and migrating to poppies, mangolds, dahlias, etc. for the summer generations; the other starting on dock and migrating to broad beans for the summer. Theobald's statements indicate that he depended mainly upon structural characters to determine the identity of the forms occurring on the winter and summer hosts. He gave the specific names which he considered to be definitely established as synonyms, as well as other possible synonyms, a comprehensive list of food plants, descriptions of the apterous viviparous female, the nymph, and the winged viviparous female. He also called attention to the differences in color of similar forms on different hosts and to differences in number of antennal sensoria in the winged viviparous female.

In America, scarcely any biological observations of *Aphis rumicis* founded upon experimental data have been published. Osborn and Sirrine (65) by means of transfer tests established the cycle from *Euonymus* to some of the summer food plants. Ohlendorff (62) in an unpublished manuscript outlined the first born generation series on *Euonymus europæus* and *Viburnum opulus* for one season, a description of forms, and a limited number of transfer tests which have been discussed in another section of this paper.

In England, Davidson (15-20) has recently published a series of papers dealing with several phases of the biology of *Aphis rumicis*. His studies include a short description of the adult

forms, a generalized life-cycle with *Euonymus* as the winter host, detailed transfer experiments on many varieties of beans, rearings to determine causal factors which determine the appearance of winged forms and sexes, and a study of the sources of food supply in the plant tissues.

Attention is called to the fact that this paper presents the first published record of detailed life history data, including first-born series, the detailed information on reproduction derived from these records, and the complete life-cycle on herbaceous plants. Practically all of the transfers presented are new since they include the common hosts of *Aphis rumicis* in the Eastern and Central United States.

ECONOMIC HISTORY AND DISTRIBUTION

In Foreign Countries: Evidently the first mention of this aphid as an insect of economic importance was by Scopoli (79) who, in 1763, noted the fact that colonies of *Aphis fabæ* rendered the broad bean, *Vicia faba*, sterile. Other early European entomologists included it under the name of *Aphis rumicis* or one of the numerous synonyms in their lists, but made no particular reference to it as a pest upon plants of economic importance. In 1815, Kirby and Spence (48) called attention to it, under the name of *Aphis fabæ*, as a pest on beans. Curtis (13), in 1860, gave an interesting account of the ravages of *Aphis rumicis* as follows: "In 1833, the beans were almost totally destroyed in Yorkshire. In 1841, they (the aphids) were abundant in my garden near the Regents' Park; but in 1842 I never saw one on the spot, yet the beans around Sandgate in the same year were very much injured by them. On the 5th of June, 1846, I could only find apterous specimens on broad bean tops; but on the 11th I detected some winged specimens and the beans in the potato rows were smothered with them, whilst those in a separate bed were free and by topping them the crop escaped."

Buckton (2) spoke of the common names, collier and black dolphin, given to this aphid by the "rustics". He said, "the stalks of the broad bean also are very liable to be similarly encrusted by them, and then both the garden and the field crops are totally destroyed. In 1854, its ravages in the turnip fields of Yorkshire were very marked, many hundred acres being entirely ruined." Theobald (88) said that in England *Aphis rumicis* is best known as a bean and mangold pest. He spoke of the fact that

the numerous individuals frequently swarmed over the young pods of the broad bean and destroyed them. He recorded the fact that he had seen whole beds of Shirley poppies, and also the tops of onions and leeks killed by this aphid.

In America: *Aphis rumicis* is generally considered to be indigenous to the Old World. We have no data which give us any hint as to the date of its introduction into America. Fitch (32), in 1870, included *Aphis rumicis* among the injurious insects reported from New York. An unpublished note by Dr. Fitch (33), telling of injury to *Euonymus*, is of interest in this connection: He wrote as follows: "*Aphis evonymi* Fab. Trees killed by it—July 9, 1873.—A spindle tree in my front yard had every leaf upon it withered and the tree died over a month ago. A large spindle tree in front of Judge Allen's house in Salem village, some 12 feet high with large spreading limbs, has its leaves mostly dropped off and the few remaining ones rolled up and wilted past recovery, and the tree is killed beyond hope of its surviving this disaster." Thomas (93) gave the synonymy, food plants then reported, and a description of the viviparous forms in his eighth Illinois report for 1878. The species was not listed by Riley and Monell (73), in 1879, as having been taken by them in the territory west of the Mississippi River. Oestlund (60) recorded it from Minnesota in 1887, as occurring on *Chenopodium album* and *Rumex crispus*, and in 1893 Osborn and Sirrine (65) described its occurrence on *Euonymus*, Dock, and *Chenopodium album*. In 1895, Gillette and Baker (38) listed it from Colorado on *Rumex crispus*. In 1908, Sanderson (75) said, "The bean aphid caused injury to beans in Massachusetts and Wisconsin; to celery, horseradish, and strawberries in California; and to rhubarb, beets and broad beans in New Jersey". Gillette (37), in 1910, published collection records of *Aphis rumicis* from Oregon, Illinois, New York and Washington, D. C., taken on *Rumex crispus*, garden beets, yellow dock, burdock, and *Chenopodium album*. He did not speak of the aphid as of particular economic importance. Britton (8) in 1916, stated that this insect had caused some injury in a field of seed beets in Connecticut. The infestation was chiefly around the edges of the field and plants of *Chenopodium album* along the borders of the field were also found to be infested.

Headlee (44) called attention to an outbreak of this aphid on beans in New Jersey in 1916. Cory (11), in 1918, said that it

was a serious pest in places on bush Lima beans in Maryland, and made the statement that the species migrated from snowball to dock in the spring. He gave no experimental data to substantiate this statement. Orton and Chittenden (64), in 1917, listed this insect as a pest of beans in all parts of the United States, especially on early beans in California. Other workers who have reported it as a pest on beans in the United States include Smith (8) in Virginia, Talbert (86) in Missouri, Stewart (83) in Utah, DeOng (24), Essig (25), and Gilbert and Popenoe (36) in California.

In 1905, Fletcher (34) noted the fact that *Aphis rumicis* was a serious pest on horse beans in Europe, but that it was only occasionally serious in Canada since the crop was little grown there. Reports in 1909 and 1917 by Bethune (5, 6) tell of the difficulty in obtaining satisfactory crops of Windsor Beans and horse beans in Canada due to the attacks of this black aphid. Sanderson (76), O'Kane (63), and Crosby and Leonard (12) listed this aphid as a pest of beans in their texts.

The following observations may be drawn from these representative reports of the occurrence of *Aphis rumicis* in Europe and in North America. The earliest records give various indigenous weeds and shrubs as the hosts of this aphid. Reports indicating that the species was of economic importance are found first in European literature and only in comparatively recent years in North America. The reports of severe infestations of an economic nature in North America have come from sections of the country where some variety of beans is grown as a staple crop, with occasional reports on *Euonymus*.

Distribution records include England, Italy, France, Belgium, Germany, Holland, Sweden, Russia, Egypt, Japan, Formosa, Canada, and practically all of the United States.

SYNONYMY

Aphis rumicis Linnæus

- 1758. *Aphis rumicis* Linnæus, Syst. Nat., Ed. X, I, 451.
- 1746. *Aphis rumicis* Linnæus, Fn. Suec., 217.
- 1758. *Aphis craccæ* Linnæus, Syst. Nat., Ed. X, I, 452.
- 1763. *Aphis viburni* Scopoli, Ent. Carn., 136.
- 1763. *Aphis fabæ* Scopoli, Ent. Carn., 139.
- 1775. *Aphis aparines* Fabricius, Syst. Ent., 735,
(*nec aparines* Fab. Oestlund).

1775. *Aphis euonymi* Fabricius, Syst. Ent., 736.
 1775. *Aphis atriplicis* Fabricius, Syst. Ent., 737,
 (*nec atriplicis* Linn.).
 1776. *Aphis papaveris* Fabricius, Gen. Ins., 303.
 1781. *Aphis viciæ* Fabricius, Spec. Ins., II, 390.
 1801. *Aphis thlaspeos* Schrank, Fn. Boic., II, 118.
 1802. *Aphis armata* Hausmann, Ill. Mag., I, 439.
 1841. *Cinaria rumicis* Mosley, Gard. Chron., I, 747.
 1847. *Viburnifex* Amyot, Ann. Soc. Ent. Fr., 2me.
 Serie, V, 478.
 1847. *Evonymaphis* Amyot, Ann. Soc. Ent. Fr., 2me.
 Serie, V, 478.
 1847. *Rumicifex* Amyot, Ann. Soc. Ent. Fr., 2me.
 Serie, V, 478.
 1847. *Meconaphis* Amyot, Ann. Soc. Ent. Fr., 2me.
 Serie, V, 478.
 1847. *Craccifex* Amyot, Ann. Soc. Ent. Fr., 2me.
 Serie, V, 478.
 1852. *Aphis hortensis* (Fab.) Walker, List Homop.
 Brit. Mus., IV, 981.
 1879. *Aphis atriplicis* (Linn.) Buckton, (in part), Mon.
 Brit. Aphides, II, 87.
 1919. *Aphis euonomi* (Fab.) Swain, U. Calif. Publ.
 Ent., III, No. 1, 101.

Aphis rumicis was originally named and described by Linnæus in 1746, in his first edition of the Fauna Suecica (49). The description from page 217 is as follows:

708. *Aphis Rumicis*

Habitat in Rumicibus 293. 295.

Descr. Corpus nigro-æneum. Antennæ nigræ vel albæ apicibus nigris. Pedes albidi geniculis nigris. Cauda acuminato-cornuta. Alarum basis virescens; Appendiculi atri, filiformes, longitudine caudæ.

Linnæus did not repeat this description in Systema Naturæ, Edition X, 1758 (50), but referred to the description in Fauna Suecica. He also listed *Aphis craccæ* in Systema Naturæ, Edition X, but the description of the species was published in Fauna Suecica, Editio Altera Auctior, 1761 (51). Kaltenbach redescribed *craccæ* under the same name in 1843 (46). After an examination of the material determined as *craccæ* at Washington and a con-

sideration of the original description and that of Kaltenbach, I have placed *cracca* as a synonym of *rumicis*.

Scopoli (79), in 1763, described a black aphid from *Viburnum* under the name of *Aphis viburni*. This has been accepted as a distinct species by most workers, but Hunter (42) considered it to be a synonym of *rumicis*. Although Theobald wrote me that *rumicis* did not occur on *Viburnum opulus* in England, Mordwilko recorded it (*evonymi*) from Russia, and Passerini listed it (*papaveris*) from Italy on this host. In America, Essig, Patch, and Wilson have recorded *rumicis* from *Viburnum*. Essig (25) published the following note in reference to *rumicis*:—"H. F. Wilson believes this species to be *A. viburni* Scop." Kaltenbach stated that the character which separated *viburni* from *rumicis* (*evonymi*) was the presence of a row of marginal spines or tubercles on the abdomen of the larva of *viburni*, which were absent on *evonymi*, but that the winged forms of the two species could scarcely be distinguished. This character is hardly of specific value since I have found wide variation in the number and prominence of these tubercles on larvæ of *rumicis* from *Viburnum*, *Rumex*, *Arctium*, and *Tropæolum*. The tubercles on segments one and seven are fairly constant, but there is considerable variation in the size of the tubercles on the intervening segments. Theobald (89) and Haviland (41) have suggested that *Aphis grossulariæ* Kalt. may be *viburni* Schr., but this is hardly the case since Kaltenbach's description of *grossulariæ* calls for an aphid with cornicles and cauda greenish-yellow, while in *viburni* they should be black. After a consideration of my results from transfer tests and cross-copulation experiments, and the examination of my own material, I have reached the conclusion that Scopoli described the spring generations of *Aphis rumicis* on one of its primary hosts and therefore I have included *viburni* as a synonym. Scopoli (79) also described forms from *Vicia faba* under the name of *Aphis fabæ*. Kaltenbach and Passerini listed *fabæ* as synonymous with *A. papaveris* which is considered in this paper to be a synonym of *rumicis*. Schouteden, Theobald and others have placed *fabæ* as a synonym of *rumicis*. My own material and some received from Theobald taken on *Vicia faba* is most certainly *rumicis*.

In 1775, Fabricius (28) described, as new, three species which are now considered to be synonymous with *Aphis rumicis* by many workers; i. e. *Aphis aparines* from *Galium aparine*, *Aphis euonymi*

from *Euonymus europæus*, and *Aphis atriplicis* on *Atriplex hortensis*. I have concluded that Fabricius in his original description of *aparines* and Schrank in a later description referred to *rumicis*. Kaltenbach incorrectly credited the authorship of *aparines* to Schrank in listing it as a synonym of *A. papaveris*. Later authors evidently followed Kaltenbach in designating Schrank as the author. Schouteden and Theobald listed *aparines* as a synonym of *rumicis*. I found the following in an unpublished note by Dr. Asa Fitch (33). "Specimens taken on *Galium* vines, side of meadows on under side of leaves. Nov. 1870, is not this the *Aphis rumicis* Linn., the *A. aparines* Fab., the *A. galii* Schrank? Dec. 8, 1870, This I have scarcely a doubt is the *Rumicis*." *Aphis aparines* Fab. of Oestlund is evidently a distinct species distinguished from *rumicis* by absence of tubercles on the prothorax and smaller number of sensoria on the antennæ.

I have taken forms in spring and fall on two species of *Euonymus* which fit the descriptions of *A. euonymi* Fab. as given by Fabricius, Schrank, Koch, and Kaltenbach. I have not been able to separate these specimens on the basis of structural characters or biology from forms taken on the same dates from *Viburnum opulus*, *Chenopodium album*, *Rumex crispus* and other host plants of *A. rumicis*. I have also proven to my own satisfaction, by numerous transfers and cross-copulation tests, the identity of the form from *Euonymus* with that from numerous other host plants and thus regard *euonymi* as synonymous with *rumicis*. Fabricius described *Aphis atriplicis* as a black aphid infesting *Atriplex hortensis*. Linnæus had previously used the name *atriplicis* for a green aphid which caused the leaves of *Atriplex* to roll longitudinally and form boat-shaped galls. The description of *A. atriplicis* Fab. agrees with that for *A. rumicis* Linn. and since *rumicis* is found on species of *Atriplex* at the present time, I have considered *atriplicis* Fab. to be a synonym.

In 1776, Fabricius (29) described forms from *Papaver somniferum* as *Aphis papaveris*. This name has been considered to be synonymous with *rumicis* by Schouteden, van der Goot, Theobald, and others. I have compared material from England and California from the poppy with my own collections of *Aphis rumicis* made in Pennsylvania and can distinguish no more than seasonal differences. *Aphis viciae* was first used by Fabricius (30) in 1781, but he credited Linnæus with the authorship, citing Fauna Suecica,

species number 986. This citation is *Aphis craccæ* Linn. as indicated by Linnæus' practice of designating the name of the species described in the margin of the page. As I have previously indicated, *A. craccæ* is considered to be a synonym of *A. rumicis* and thus *A. vicæ* Fab. also goes into synonymy.

I have followed Schouteden, Theobald, and others in listing *Aphis thlaspeos* Schrank as a synonym of *A. rumicis* on the basis of the original description and the fact that *rumicis* is known to occur on shepherd's purse, the host from which Schrank's material was collected. Schrank (77) called attention to the similarity in appearance of *thlaspeos* with the species on dock, *A. rumicis*, although he considered them to be distinct.

Several workers have placed *Aphis armata* Hausm. as a synonym of *rumicis*. After a careful consideration of Hausmann's original description (40) it seems certain that he referred to *A. rumicis* and I have consequently listed *armata* as a synonym. *Cinaria rumicis* Mosley has been correctly listed by various authors as synonymous with *Aphis rumicis*. Mosley (57) adopted the suggestion of Curtis and used the name *Cinaria* for a section of the genus *Aphis*.

In 1847, Amyot (1) proposed as new names for *A. rumicis* and other names which I have listed as synonyms, *Rumicifex*, *Viburnifex*, *Evonymaphis*, *Meconaphis* and *Craccifex*. As there seem to be no reasonable grounds for making such a change, I have considered these as synonyms of *A. rumicis*.

Walker (98) listed *Aphis hortensis* Fab. as a synonym of *rumicis*, but his citation refers to *atriplicis* Fab. Although Fabricius wrote the name *Aphis atriplicis hortensis* at the beginning of the description, he designated *atriplicis* as the specific name in the margin according to his usual practice. Since *atriplicis* Fab. is a synonym of *rumicis*, *A. hortensis* Fab. of Walker also becomes a synonym.

Aphis atriplicis Linn. of Buckton (2) is in part synonymous with *Aphis rumicis*. His descriptions of varieties 1 and 2 of the apterous viviparous female and that of the winged viviparous female certainly refer to *rumicis* on *Chenopodium*.

Swain (84), in 1919, published excellent descriptions of forms of *Aphis rumicis* from various host plants. He raised the question as to the identity of *A. rumicis* Linn. and proposed that *rumicis* Linn. of American and late European workers should be considered as synonymous with *Aphis euonomi* Fab. He gives, as the basis

TABLE I—COMPARISON OF SPECIES

Species and Host	III	Antennae IV	VI	Cornicles	Cauda	Hind Tarsus
<i>Aphis rumicis</i> Linn. <i>Rumex crispus</i> Spring migrant	Longer than IV Slightly shorter than VI unguis 9 - 15 sensoria	Equal to V or slightly longer	Unguis 3 base Base nearly equal to hind tarsus	Shorter than III, Equal to IV Almost 2x hind tarsus	Slightly more than $\frac{1}{2}$ of cornicles Slightly longer than hind tarsus	Slightly longer than VI base
<i>Aphis laburni</i> Kalt. <i>Genista tinctoria</i> Det. Pergande	Longer than IV Slightly shorter than VI unguis 4 - 5 sensoria	Equal to V	Basal area large Unguis 2x base.	Shorter than VI base about $\frac{1}{2}$ III	Longer than cornicles by $\frac{1}{2}$	Shorter than VI base, equal to cornicles
<i>Aphis laburni</i> Kalt. <i>Laburnum vulgare</i> Det. Pergande	Equal to or slightly longer than IV. Equal to VI unguis 4 - 6 sensoria	Equal to V	Unguis 2x base.	Longer than III or VI unguis		
<i>Aphis hederae</i> Kalt. <i>Hedera helix</i> Summer migrant	Equal to IV Hardly more than $\frac{1}{2}$ VI unguis 3 sensoria	Equal to V	Unguis 3x base Base shorter than hind tarsus	Shorter than III or IV. Longer than hind tarsus and VI base by $\frac{1}{2}$	Shorter than cornicles, equal to hind tarsus. Restricted at base.	About equal to VI base

for this proposal, the distinction as to host plants and color of the winged form. I have quoted the original description of Linnæus in which it will be noted that the color given for the winged form is "black-bronze". I have often taken specimens of *rumicis* on *Rumex* which exhibited this blackish-brassy tinge to the body due to the obscure dark olive cast from the body contents. Nor can it hardly be argued that *rumicis* of American authors is not *rumicis* Linn. just because *Rumex* is the only host mentioned in the original description. In the history of aphidology, probably the majority of species have been described from a single host many years before the complete life history was understood or the alternate hosts, if any, were known. I have examined some of Swain's material and find that it agrees with similar forms which I have taken in Iowa and Pennsylvania, and with material from Theobald in England. Therefore, I feel that we are not justified in making the change proposed by Swain, and since his specific name, *euonomi*, varies in spelling from the original *euonymi*, it must be considered as a synonym of *Aphis rumicis* Linn.

Several other names have been incorrectly listed by various authors as synonyms of *A. rumicis*. Schrank's *Aphis gallii Scabri* (77) I consider to be distinct from *rumicis* since his description of the wingless viviparous female from bristly *Galium* calls for an aphid with "cornicles and cauda short appearing as scarcely more than elevated spots."

Aphis dahliæ Mosley has been incorrectly cited as a synonym since Mosley (57) described an amber-colored aphid with legs, tubercles (cornicles) and antennæ of the same color as the body.

TECHNICAL DESCRIPTIONS

Egg: (Plate VIII, A) Elongate, cylindrical, slightly flattened along one side, bluntly rounded at the ends. Olive-green when first deposited, soon turning to shiny black. Average length 0.5 mm.

Stem Mother: (Plate V, I). Velvet black tinged with olive. Body oval, broadly rounded behind. Head without ocelli, with a few scattering hairs. Eyes black, with prominent accessory tubercles. Antennæ with five segments. Prothorax distinct with pair of lateral tubercles. Mesothorax and metathorax merged in outline with the abdomen which is arched and swollen. Lateral tubercles on first and seventh abdominal segments and sometimes on intervening segments. Cornicles black, tubular, imbricated,

flanged at the mouth. Cauda black, distinctly conical, not tapering as in apterous viviparæ, furnished with several curved hairs on the margin. Legs shorter and stouter than in apterous viviparæ but similarly colored. Described from specimens taken on *Viburnum opulus* in April and transferred to *Rumex crispus* for generation series. Measurements: Length of body, vertex to tip of cauda, 1.896 to 2.292 mm.; Antennæ, I, 0.068 mm.; II, 0.051 mm.; III, .310 to 0.379 mm.; IV, 0.137 to 0.172 mm.; V base, 0.103 mm.; V unguis, 0.103 to 0.137 mm.; Cornicle, 0.155 to 0.206 mm.; Cauda, 0.172 mm.; Hind tarsus, 0.103 to 0.120 mm.

First Instar: (Plate IV, G). (Approximately 7 hours old). Head dark purplish green with slight longitudinal median carina and narrow lateral light-green bands bordering the eyes, about four hairs on vertex; Eyes dark red each with lateral tubercle of five or six facets. Antennæ pale, faintly tinged with green, four-segmented, the distal end of III and all of IV dusky. Prothorax olive-black with a lateral tubercle on each side. Mesothorax, metathorax, and abdomen olive-green with a purplish tinge, entirely covered with faint, whitish bloom. Abdomen with a distinct submarginal groove on each side extending back to the cornicles in which are distinct pits, segmentally arranged. Sides of each abdominal segment bearing a small hair. First and seventh segments with a small lateral tubercle on each side. Lateral tubercles often present on intervening segments. Cornicles dusky-black, short, tubular. Cauda black, short, triangular, with fringe of about five hairs on each side. Legs stout, clumsy, whitish, faintly tinged with green, the distal ends of femora and tibiæ and all of tarsi blackish. Femora sparsely hairy, tibiæ distinctly hairy. Measurements from specimens freshly mounted in balsam: Body length, 0.756 mm., width, 0.369 mm.; Cornicles, length, 0.047 mm., width, 0.035 mm.; Antennæ, I, 0.044 mm.; II, 0.035 mm., III, 0.140 mm., IV base, 0.061 mm. VI unguis, 0.140 mm.

Second Instar: (60 to 70 hours old). Similar to first instar, but darker with five-segmented antennæ, longer cornicles, and lateral tubercles on abdomen more distinct. Measurements from specimens freshly mounted in balsam: Body length, 0.739 mm., width, 0.404 mm.; Cornicles, length, 0.052 mm., width, 0.035 mm.; Antennæ, I, 0.052 mm., II, 0.035 mm., III, 0.088 mm., IV, 0.070 mm., V base, 0.052 mm., V unguis, 0.158 mm.

Third Instar: (170-173 hours old). Similar to first instar with five-segmented antennæ. Measurements from specimens freshly

mounted in balsam: Body length, 0.950 mm., width, 0.528 mm.; Cornicles, length, 0.073 mm., width, 0.038 mm.; Antennæ, I, 0.051 mm., II, 0.044 mm., III, 0.140 mm., IV, 0.082 mm., V base, 0.070 mm., V unguis, 0.170 mm.

Fourth Instar, Apterous Form: (208-216 hours old). Similar to first instar with six-segmented antennæ. Measurements from specimens freshly mounted in balsam: Body length, 1.443 mm., width, 0.862 mm.; Cornicles, length, 0.114 mm., width, 0.070 mm.; Antennæ I, 0.070 mm., II, 0.056 mm., III, 0.158 mm., IV, 0.132 mm., V, 0.132 mm., VI base, 0.088 mm., VI unguis, 0.246 mm.

Fourth Instar, Pupa: (Plate IV, F): General shape elongate-oval. Head and prothorax black with greenish-brown hue, slightly powdered. Pair of lateral tubercles on prothorax. Prominent lobes of mesothorax and the entire metathorax grayish-green. Abdomen black shaded with olive, with prominent white pulverulent patches as follows: a pair of round areas on the first segment, a broad band, often broken into paired spots, on either side of a median line on each of the next three segments, pairs of spots close together on the sixth and seventh segments and faintly showing on the eighth segment. These white areas are absent from fifth segment. Lateral tubercles present on the first and seventh abdominal segments. Antennæ, wing-pads, cornicles, and cauda black. Legs colored as in winged viviparous female. Measurements: Length of body, 2.103 mm.; Antennæ, I, 0.046 mm.; II, 0.046 mm., III, 0.241 mm.; IV, 0.172 mm.; V, 0.163 mm.; VI base, 0.094 mm.; VI unguis, 0.258 mm.; Cornicles, 0.181 mm.; Cauda, 0.120 mm.; Hind tarsus, 0.137 mm. Described from specimens on *Chenopodium album* and *Rumex crispus*, October 1923. The pupæ of the males are comparatively smaller in size but resemble in color the pupæ of the winged viviparæ as given above.

Winged Viviparous Female, (Plate II, F): Morphological characters:—Antennæ, measurements given in Table II.; Segments III to VI inclusive imbricated, armed with scattering hairs, which are about equal in length to width of each segment on which they are borne; III bearing 10 to 22 round sensoria unevenly distributed over the segment, the distal 4 or 5 arranged in a row, IV with 0 to 7 sensoria, V with the usual prominent sensorium near the distal end and sometimes bearing an additional proximal one, base of VI with the usual compound sensorium. The numbers of sensoria vary on the corresponding segments of the two antennæ of the same indi-

vidual. There is also a consistent variation in the number of antennal sensoria of the spring and summer migrants and of the fall migrants or sexuparæ alatæ, III of the fall migrant usually bearing about 4 more secondary sensoria than III of the spring or summer alatæ and IV of the spring forms usually without sensoria while IV of the fall form may have as many as 7 or 8, and V of the fall form may also bear 1 or 2 in addition to the usual primary sensorium. Eyes large, with prominent lateral tubercle. A single ocellus contiguous to inner margin of each eye a little distance behind base of antenna, a third ocellus at center of vertex, slightly protruding. Extending back from the median ocellus is a slight carina. Prothorax distinct, bearing a pair of prominent lateral tubercles. Præscutum, scutellar lobes, and scutellum distinct. Abdomen ovate, suddenly tapering behind, lateral tubercles always present on segments 1 and 7 and sometimes on the other segments. Cornicles imbricate, tubular, tapering slightly, with flange at the mouth, length 0.224 to 0.310 mm., slightly shorter in fall migrants. Anal plate rounded, beset with numerous hairs and short spines. Cauda cylindrical, with bluntly pointed tip, numerous short spines and 4 to 5 long curved hairs on each side, length 0.137 to 0.206 mm., shorter in fall migrant. Legs slender, with numerous short hairs, length of hind tarsus 0.123 to 0.146 mm. Length of body, vertex to tip of cauda, 1.534 to 2.068 mm. The fall migrants are slightly longer, as will be seen in accompanying table.

Color characters:—General color to unaided eye jet black with legs dirty yellow. Under the binocular, head and thorax shining black; eyes brownish-black, ocelli lighter; antennæ dark brown to black with lighter area at base of III; labium yellow with black tip; legs dusky yellow with middle and hind femora, distal one-fourth of tibiæ and tarsi black. Wings transparent, veins brownish with stigma smoky. Abdomen varying from deep olive-green to blackish-brown with black dorsal markings which become distinct in balsam mounts as follows: median black bands on each abdominal segment, those on the first six segments separate and distinct, with those on the seventh, eighth and ninth confluent. Black patches on the lateral edges of each segment separated more or less from the median bands, those on the sixth segment more extensive than the others forming distinct black areas behind the base of each cornicle. The extent of these black markings on the abdomen is subject to considerable variation among different in-

TABLE II—COMPARATIVE MEASUREMENTS OF WINGED VIVIPAROUS FEMALES

Spring Migrant	Length mm.	III mm.	IV mm.	V mm.	VI base	VI unguis	Corn.	Sensoria		
								III	IV	V
<i>Rumex</i> , May	1.672	0.344	0.241	0.241	0.120	0.396	0.232	15	0	0
"	1.534	.327	.241	.241	.112	.362	.224	12	0	0
"	1.620	.327	.258	.241	.120	.344	.258	11	0	0
"	1.724	.362	.275	.258	.137	.379	.258	14	0	0
"	1.586	.327	.258	.241	.120	.396	.241	11	0	0
"	2.034	.396	.293	.258	.120	.344	.310	13	0	0
"	1.948	.362	.275	.258	.120	.379	.310	12	0	0
<i>Euonymus</i> , May	2.068	.344	.258	.224	.120	.362	.275	11	0	0
"	1.982	.353	.258	.215	.112	.310	.241	12	0	0
<i>Viburnum</i> , May	1.775	.327	.258	.241	.129	.353	.310	12	0	0
"	1.982	.362	.310	.224	.120	.310	.293	16	1	0
Fall Migrant										
<i>Rumex</i> , Nov.	2.552	.352	.272	.255	.123	.360	.228	20	7	0
"	2.358	.360	.246	.237	.114	.316	.237	15	7	0
"	2.200	.334	.264	.246	.140	.281	.228	22	3	1
<i>Chenopodium</i> , Oct.	2.252	.343	.258	.220	.123	.316	.193	17	4	0
"	2.534	.369	.220	.228	.123	.308	.193	17	3	0
"	2.376	.360	.281	.246	.123	.316	.228	18	3	1
<i>Arctium</i> , Nov.	2.464	.343	.281	.246	.123	.369	.220	20	5	0
<i>Philadelphus</i> , Oct.	2.129	.352	.264	.237	.132	.360	.237	18	8	0

dividuals of the same generation on the same host plant, some specimens having only disconnected black areas in place of median dorsal bands. Cornicles black; cauda green at base, distal half black. General body color of fall migrants as noted from unmounted material varied with the host. Specimens from *Euonymus*, *Philadelphus*, and *Hydrangea* were blackish-brown while those taken on *Chenopodium* and *Rumex* at the same date were of a deep olive cast. Described from specimens taken on *Rumex crispus* and *Euonymus atropurpureus* at Bustleton, Pa., in May. Measurements from balsam mounts.

Apterous Viviparous Female, (Plate III, B): Morphological characters:—Antennæ shorter than body; segments V and VI distinctly imbricated, III and IV faintly so; a single primary distal sensorium on V, the usual compound sensorium at base of VI unguis. Eyes large with ocular tubercle at the outer posterior angle. Prothorax with a pair of distinct lateral tubercles, other two thoracic segments more or less merged in outline with the abdomen. Abdomen ovate, swollen, often with segmentation obscure. Lateral tubercles present on the first and seventh abdominal segments, sometimes present on intervening segments but not as distinct, a submarginal row of pits on each side of abdomen arranged segmentally in front of the cornicles. Cornicles imbricated, cylindrical, tapering slightly toward the mouth which is flanged, length 0.224 to 0.396 mm. Anal plate hemispherical, furnished with hairs and short spines as is the genital plate. Cauda cylindrical, tapering to a blunt point, four or five curved hairs on each margin, covered with small spines, length 0.172 to 0.275 mm. Legs slender, sparsely hairy, length of hind tarsus 0.114 to 0.137 mm. Length of body, vertex to tip cauda, 1.758 to 2.465 mm. In the fall, the apterous forms (sexuparæ) are relatively larger than the summer apteræ but the cornicles and cauda are shorter.

Color characters:—General color to the unaided eye dull black, sometimes with white pulverulent patches on the back. Very often, in mid-summer, individuals have a distinct olive green cast to the abdomen, especially when reared in shaded situations. In the fall, individuals of a shiny bronze color are to be found in colonies on *Rumex crispus* and *Arctium lappa*. Many of these forms when examined under the microscope are found to be intermediates. Specimens of the summer forms on balsam mounts usually show a row of small black submarginal spots marking the location of the

pits on either side of the body and a black streak at the base of the cauda. Antennæ dirty yellow with I, II, distal end of V, and all of VI blackish. Eyes brownish-black. Legs dirty yellow with distal two-thirds of middle and hind femora, distal one-fourth of tibiæ, and tarsi black. Individuals which had three to five pairs of pulverulent patches on the abdomen were reared and collected in the fall. Described from specimens taken on *Rumex crispus* in June and *Rumex crispus* and *Arctium lappa* in October, 1923, at Bustleton, Pa.

TABLE III
COMPARATIVE MEASUREMENTS OF APTEROUS FEMALE

	Length Body	III	IV	V	VI base	VI unguis	Corn.
Spring Forms	mm.	mm.	mm.	mm.	mm.	mm.	mm.
<i>Rumex</i> , June	1.89	.0370	.0284	.0258	.0137	.0396	.0310
" "	1.75	.396	.293	.241	.120	.310	.344
<i>Chenopodium</i> , June	2.46	.448	.249	.224	.129	.327	.344
" "	2.06	.413	.275	.241	.120	.379	.396
Fall Forms							
<i>Rumex</i> , Nov.	2.37	.387	.228	.211	.105	.299	.228
" "	2.56	.316	.202	.184	.105	.281	.220
" "	2.42	.316	.246	.220	.114	.325	.255
<i>Chenopodium</i> , Nov.	2.46	.316	.228	.211	.114	.325	.264
" "	2.28	.352	.228	.228	.114	.255	.211
" "	2.62	.348	.228	.193	.114	.272	.228

Oviparous Female, (Plate V, B): Morphological characters:—Antennæ: I, 0.044 to 0.061 mm.; II, 0.035 to 0.047 mm.; III, 0.184 to 0.220 mm.; IV, 0.096 to 0.158 mm.; V, 0.123 to 0.158 mm.; VI base, 0.096 to 0.105 mm.; VI unguis, 0.176 to 0.237 mm.; Segments V and VI distinctly imbricated, IV faintly so. A very few hairs along the entire length of the antennæ, scarcely as long as width of respective segments, a single circular sensorium at distal end of V and the usual compound sensorium at the base of VI unguis. Eyes distinct with the usual lateral accessory eye on each. Prothorax distinct with a pair of distinct lateral tubercles. Other thoracic segments somewhat indistinct and merged in outline with the abdomen. Abdomen ovate, more tapering caudad than the apterous viviparous female, a pair of lateral tubercles present on first and third abdominal segments, smaller tubercles sometimes found on other segments. Cornicles cylindrical, imbricated,

flanged at the mouth, length 0.105 to 0.158 mm. Cauda conical with bluntly rounded tip, armed with numerous papillæ and several long curved hairs, length 0.096 to 0.123 mm. Anal plate hemispherical, papillate, with several distinct hairs. Genital plates papillate, two in number. Legs hairy, the hind tibiæ flattened and bearing numerous small round sensoria. Length of hind tarsus 0.105 to 0.123 mm. Length of body, vertex to tip of cauda, 1.408 to 1.988 mm.

Color Characters:—General color to unaided eye dull black, suffused with olive green or reddish-brown, depending upon the host upon which they are feeding. Those from *Euonymus* and *Philadelphus* had the reddish cast while those on *Viburnum*, *Maclura pomifera*, *Chenopodium album*, and *Rumex crispus* had the olive green cast. Antennæ blackish with the exception of segments III and IV which are dirty yellow in color. Cornicles and distal half of cauda black. Anal and genital plates black. First and second pair of legs yellowish with tips of tibiæ and tarsi black. Hind pair of legs black. Described from specimens taken on *Euonymus alatus* at Bustleton, Pa., in November. Measurements from balsam mounts.

Winged Male, (Plate II, A): Morphological Characters:—Antennæ; Segments III to VI inclusive are imbricated, armed with scattering hairs which are more prominent than those on the alate female; III bears 24 to 41 prominent sensoria, unevenly distributed, IV with 15 to 25 sensoria, V with 7 to 16 sensoria in addition to the usual prominent sub-apical sensorium, base of VI with the usual compound sensorium at the base of the unguis, the numbers of sensoria on segments III, IV, and V may vary considerably, as shown in Table IV. Eyes large, each with prominent lateral tubercle of several facets. A single ocellus on either side of head, contiguous to inner margin of eye and somewhat removed from base of antennæ, a third prominent ocellus, somewhat protruding at center of vertex. Prothorax distinct, slightly narrower than width of head, bearing a pair of prominent lateral tubercles. Præscutum, the two scutellar lobes, and the scutellum prominent and distinct. Abdomen ovate, relatively shorter antero-posteriorly than in alate female, lateral tubercles present on 1st, 7th and sometimes other abdominal segments. Cornicles distinctly imbricated, tubular, with distinct flange at mouth, length 0.088 to 0.149 mm. Anal plate rounded, with numerous fine hairs. Cauda cylindrical, tapering distally to a blunt point, with 6 to 8 curved hairs, length

0.086 to 0.140 mm. Legs slender, hairy. Length of hind tarsus 0.103 to 0.137 mm. Length of body, vertex to tip of cauda, 1.137 to 1.900 mm.

Color characters:—General color to the unaided eye is shining black with legs lighter. Under the binocular the head and thoracic segments are seen to be shining black, with eyes brownish-black. Labium dusky yellow with black tip. Antennæ deep brown. Legs dusky yellow with femora of middle and hind legs, distal tips of front femora, one-fourth of all tibiæ, and all tarsi black. Wings transparent with blackish veins and smoky stigma. Abdomen almost black with an olive-green tinge through which the jet-black markings are discernible. Black bands, irregular in outline and extent, on each of the first five segments, sometimes reaching the two lateral margins but often broken to form a central band and lateral spots. Behind the cornicles, the entire dorsum of each segment is black. Cornicles and cauda black. Described from specimens taken on *Chenopodium album* and *Euonymus alatus*, at Bustleton, Pa. Measurements from balsam mounts.

TABLE IV—COMPARATIVE MEASUREMENTS OF MALES

	III	IV	V	VI	VI	Corn.	Sensoria		
	mm.	mm.	mm.	base	unguis	mm.	III	IV	V
<i>Chenopodium</i>	0.352	0.193	0.176	0.105	0.290	0.088	28	16	13
"	.334	.228	.190	.102	.334	.105	31	16	12
"	.334	.211	.176	.096	.272	.088	34	17	16
"	.334	.193	.158	.096	.264	.088	39	22	12
"	.334	.246	.220	.114	.343	.132	30	18	14
<i>Eumex</i>	.352	.311	.272	.132	.369	.149	26	17	7
"	.369	.281	.246	.123	.369	.140	30	17	7
<i>Maclura</i>	.334	.299	.237	.123	.334	.140	34	18	10
"	.325	.246	.211	.114	.334	.105	36	20	10
<i>Calycanthus</i>	.396	.313	.241	.137	.310	.103	37	25	11
"	.343	.284	.189	.094	.241	.103	35	21	8
"	.362	.262	.206	.103	.336	.120	31	25	6
<i>Euonymus</i>	.413	.310	.258	.120	.336	.137	31	22	12
"	.343	.241	.206	.103	.275	.137	25	17	11
"	.396	.275	.241	.120	.379	.103	32	17	9
"	.379	.275	.215	.103		.120	38	19	14
"	.413	.275	.241	.103	.343	.137	41	21	12

Intermediates in the Aphidæ are of interest because of their possible phylogenetic significance. Apterous forms with traces of alate characters seem to indicate that the wingless forms evolved from the winged individuals. Baker and Turner (3) stated that they had noted an intermediate in *Aphis rumicis*, but they gave

no description of the form. In my studies, intermediates of several forms were collected or reared.

Intermediate Male, (Plate III, A): Color and appearance very nearly that of the alate male. Measurements of one individual as follows: Antennæ, III, 0.413 mm. bearing 5 secondary sensoria of normal size and many microscopic sensoria, IV, 0.293 mm. bearing about 10 tiny sensoria, V, 0.258 mm. bearing about 10 tiny sensoria and the usual primary distal sensorium, VI base, 0.137 mm., unguis 0.344 mm.; Cornicles 0.155 mm., Cauda, 0.155 mm., Hind tarsus, 0.103 mm. Ocelli present on head as in alate form. Mesothorax chitinized but with only a slight indication of lobes. The wings are represented on both thoracic segments by small buds which are visible by transmitted light. A second specimen has the normal number of sensoria, i. e. III, 32; IV, 19; V, 12; and indication of thoracic lobes, and wings represented by four small pads.

Described from three specimens taken with winged males on *Arctium lappa*, October 11, 1922, Bustleton, Pa.

Intermediate Viviparous Female, (Plate V, G). General size and form of body approaching that of the apterous sexupara. Color of antennæ, cornicles, cauda, and legs similar to apterous form. Abdomen with distinct black bands segmentally arranged as in alate form, black patches present at the base of the cornicles, but absent from the abdominal margin. Rows of small black spots marking the pits same as in apterous form. Thoracic lobes distinct, præscutum and scutellum present, but reduced in size. Wings represented by four flaps projecting from the sides. A second specimen on the same slide has the black markings on the abdomen similar to those described above but not as distinct. Alate characters of the thorax exhibited in a chitinized surface and a faint groove showing a division into the two lobes. Wings indicated only by four small buds.

Described from two specimens taken on *Rumex obtusifolius*, November 3, 1923, at Bustleton, Pa. The following note was made at time of collection, "shiny, viviparous female." A third specimen collected on *Chenopodium album*, November 1, 1923, had markings similar to the first specimen described above, but had 5 secondary sensoria on segment III of antennæ, and 5 sensoria on IV, unguis of VI was aborted.

Intermediate Oviparous Female, (Plate V, H.): General form and appearance of the apterous viviparous female. Antennæ

shorter than the viviparous form but longer than the true oviparous form. Segment III, 0.275 mm.; IV, 0.172 mm.; V, 0.155 mm.; VI, base, 0.103 mm.; VI unguis, 0.224 mm. All of IV, V, and VI blackish, distinctly imbricated, III faintly imbricated. The hind tibiae are slender as in the viviparous female, but about one-fifth shorter. Three full sized ova are clearly seen within the abdomen of one specimen.

Described from three specimens reared in generation series, October, 1922, Bustleton, Pa. Two of these females mated with males taken from *Arctium lappa* in the field and the third with a male reared on *Rumex crispus*. Ova were deposited by these females on *Rumex obtusifolius*.

LIFE HISTORY STUDIES

METHODS OF STUDY

The rearing experiments were carried on at the Pennsylvania State College Field Laboratory, Bustleton, Pa., during the summers of 1920-21-22 and 23 in the insectary and in the field cages. A series was also reared from September 1921 to June 1922 in the greenhouse of the Department of Botany, State University of Iowa, Iowa City, Iowa. The insectary consisted of a shelter roof with open sides. Protection from beating rains was provided by using side curtains of thin muslin (Plate IX, A). Some of the plants were grown in a dirt bench and some were planted in seven inch pots. The soil used was a fairly rich compost of sand, clay soil, and manure. Growing potted plants were used for all generation and transfer experiments, with the exception of the generations on woody plants. Cuttings placed in water or damp sand were used for the experiments on *Euonymus*, *Viburnum*, *Hydrangea* and *Maclura*.

Two types of cages were used in the rearing work. One type consisted of ordinary glass lantern globes over the top of which thin covers of cheese cloth were fastened. The second type or field cage, the same as used by Smith (81), was made by stretching muslin over wooden frames of inch material. The corner strips extended six inches below the bottom level of the cage and, when sunk into the ground, served as anchorages (Plate IX, B). The entrance was provided by running a width of cloth around one side of the frame which had been left uncovered. When this was sewed together at the two loose ends, it formed a sleeve enveloping

the body while examinations were being made and prevented escape of winged forms or entrance of parasites. This cloth was gathered to the center and tied when the cage was closed. The cages were of two sizes, 14"x14"x30" and 30"x30"x30". Maximum and minimum temperatures were recorded throughout each season.

In the generation experiments the usual method was followed. The viviparous female was removed by means of a small brush at the end of her first day of reproduction. She was then placed on a growing plant free from aphids, and data on the number of young, etc. were thus obtained each day of her life. As Davis has suggested, the method of leaving several new-born young instead of a single individual insures, almost to a certainty, the continuation of the line. These first-born young were checked at maturity in order to determine the presence or absence of winged individuals. The series for 1923 outlined in detail in Tables VI and VIII are representative of the generation experiments of the previous three years.

FOOD PLANTS

Aphis rumicis Linn. is an exceptionally polyphagous aphid. The majority of the species of the Aphidæ are restricted in their feeding habits to a small number of plants, but this insect has adapted itself to a wide range of hosts. Wilson and Vickery (99) have listed, under *Aphis rumicis* or the synonyms included in their paper, 189 species of host plants. Patch (66, 67, 68, 70, 71) has cited, in the various parts of her Food Plant List, 17 additional hosts and in the Hemiptera of Connecticut (10) 3 other species. Swain (84) records 8 species of plants not included in the above lists and I have collection records for 9 additional hosts. This brings the total number of recorded hosts for *Aphis rumicis* to 226. A few of these may be incorrect citations since they may refer to species of aphids which have been erroneously placed as synonyms of *Aphis rumicis*. Only one other aphid approaches *rumicis* in its wide range of accepted hosts, i.e. *Myzus persicæ* Sulz., for which Wilson and Vickery list 175 food plants.

My additional records are as follows: Primary hosts:—*Calycanthus fertilis*, *Euonymus alatus*, *Hydrangea paniculata*, *Maclura pomifera*, and *Chenopodium album*; Secondary hosts:—*Aster* sp., *Chenopodium ambrosioides*, *Galinsoga parviflora*, *Polygonum scandens* var. *dumetorum*, and *Stellaria media*. Other plants upon which I have collected or reared this aphid are given in the

Seasonal History Chart (Table XII). The large number of hosts upon which this insect is able to exist accounts in part for its abundance and cosmopolitan distribution. The ultimate result of this polyphagous habit may be that several physiological species may arise which, in time will exhibit distinctive morphological characters.

TRANSFER TESTS

During the four seasons in which life history studies on *Aphis rumicis* were being conducted, considerable attention was devoted to transfers of aphids from one host plant to another at various seasons of the year. It was desirable to obtain these data for two reasons: first, to establish more certainly the specific identity of forms collected from different host plants but having no distinct morphological differences of apparent specific value; second, to verify the summer and winter host plants upon which this species lives in localities covered by these studies. The data were obtained in the following manner. The desired host plants were grown in 6 and 7 inch pots in an out-of-doors insectary. These plants were covered with lantern globes, the tops of which were covered with a single thickness of cheese cloth. Specimens were reared from ova or were collected from colonies breeding in the field or at the insectary on the host of a different species than that to be tested. In most cases several aphids were transferred to the potted plant by means of a soft brush and observations made from time to time. Whenever possible winged females were used in making the test and no experiment was considered successful until progeny of the transferred form matured and produced young. These tests necessitated the use of twenty-two species of host plants grouped in forty-three different combinations. In addition, notes were taken in the field on transfers effected by the insects themselves, under conditions which were very reliable. These transfers included combinations in addition to those used under controlled conditions. These records will be indicated as such in table V so that, unless specifically stated, the experiments as tabulated were under controlled conditions. It might be well to explain here that such experiments are of peculiar value in working out authentic hosts, since aphids are particularly selective in their feeding habits. Individuals, when placed upon plants which are not the normal food of the species, will crawl from the plants to the sides or top of the cage and remain there until they die rather than feed upon this foreign plant.

TABLE V—TRANSFER EXPERIMENTS, *APHIS RUMICIS*

Transfers to	From	Remarks
<i>Chenopodium album</i>	<i>Viburnum opulus</i>	
" "	<i>Viburnum opulus</i>	
" "	<i>Daucus carota</i>	unsuccessful
" "	<i>Dahlia</i> sp.	
" "	<i>Gladiolus</i> sp.	
" "	<i>Spinacia oleracea</i>	
" "	<i>Rumex crispus</i>	
" "	" "	
" "	<i>Arctium lappa</i>	
" "	" "	
" "	<i>Chenopodium album</i>	
" "	<i>Eheum rhapsodicum</i>	
<i>Beta vulgaris</i>	<i>Rumex crispus</i>	(Davidson, <i>R. sanguineus</i>)
" "	<i>Chenopodium album</i>	
<i>Rumex crispus</i>	<i>Rheum rhapsodicum</i>	
" "	<i>Rumex crispus</i>	(Davidson, <i>R. sanguineus</i>)
" "	<i>Begonia</i> sp.	
" "	<i>Arctium lappa</i>	
" "	<i>Dahlia</i> sp.	
" "	<i>Gladiolus</i> sp.	
" "	<i>Chenopodium album</i>	
" "	<i>Daucus carota</i>	
" "	<i>Viburnum opulus</i>	(Osborn and Serrine)
" "	<i>Euonymus atropurpureus</i>	(Davidson, <i>R. sanguineus</i>)
" "	" "	
" "	<i>Maclura pomifera</i>	
<i>Rumex obtusifolius</i>	<i>Amaranthus retroflexus</i>	
" "	<i>Pisum</i> sp.	(Ohlendorf)
" "	<i>Chenopodium album</i>	
<i>Phaseolus</i> sp.	<i>Rumex crispus</i>	unsuccessful
<i>Papaver</i> sp.	<i>Chenopodium album</i>	
<i>Mirabilis jalapa</i>	<i>Tropæolum minus</i>	
<i>Arctium lappa</i>	<i>Viburnum opulus</i>	
" "	<i>Tropæolum minus</i>	
" "	<i>Chenopodium album</i>	
" "	<i>Rumex crispus</i>	
<i>Rheum rhapsodicum</i>	<i>Viburnum opulus</i>	
" "	<i>Rumex crispus</i>	
" "	<i>Arctium lappa</i>	colony weak
" "	<i>Chenopodium album</i>	
<i>Spinacia oleracea</i>	<i>Viburnum opulus</i>	
<i>Amaranthus retroflexus</i>	<i>Pisum</i> sp.	
<i>Asparagus</i> sp.	<i>Rumex crispus</i>	
<i>Stellaria media</i>	<i>Chenopodium album</i>	
<i>Viburnum opulus</i>	<i>Chenopodium album</i>	Ova
<i>Euonymus atropurpureus</i>	<i>Chenopodium album</i>	
<i>Maclura pomifera</i>	<i>Chenopodium album</i>	field
<i>Oenothera biennis</i>	<i>Chenopodium album</i>	field
<i>Galinsoga parviflora</i>	<i>Chenopodium album</i>	
<i>Rosa</i> sp.	<i>Chenopodium album</i>	field
<i>Gladiolus</i> sp.	<i>Tropæolum minus</i>	field
<i>Dahlia</i> sp.	<i>Tropæolum minus</i>	field
<i>Pisum</i> sp.	<i>Tropæolum minus</i>	field
<i>Capsella bursapastoris</i>	<i>Chenopodium album</i>	

Osborn and Sirrine (65) made successful transfers of this aphid from *Euonymus atropurpureus* to *Viburnum opulus* and from this stock on *Viburnum* to shepherd's purse, curled dock and beans. They failed to establish aphids from *Viburnum* on *Euonymus*. It may be that in making this latter test they were using *Aphis viburniphila* Patch, another dark form on *Viburnum*. Theobald (88) reported that he had made transfers of *Aphis rumicis* from *Euonymus europæus* to broad beans (*Vicia* sp.). Swain (84) failed to secure colonies of this aphid on *Hedera helix* or *Rumex* sp. when material was transferred from *Vicia* sp. Ohlendorf (62) made successful transfers from *Philadelphus*, *Euonymus*, and *Viburnum opulus* to *Euonymus europæus* and *Viburnum opulus*. The same worker failed to make successful transfers from nasturtium to *Euonymus* or from *Rumex obtusifolius* to apple, lima bean, or turnip. He did succeed in securing colonies upon nasturtium, navy bean, and pea from stock on *Rumex obtusifolius*.

Davidson (15-20), who has done the most work with *Aphis rumicis* along this line, recorded successful transfers from *Euonymus* to broad bean, horse bean, dwarf French bean, peas, poppies, *Rumex* sp. and *Euonymus*. He also secured colonies on *Euonymus* from stock on broad bean. From material which he transferred to *Rumex* from *Euonymus*, he secured colonies by re-transfer on broad bean, horse bean, dwarf French bean, peas, poppies, *Rumex* sp., mangolds, red beets, and sugar beets.

The combinations which I used in making my tests were largely determined by the common hosts upon which I had taken colonies of *Aphis rumicis* in the field. For this reason there is a distinct departure from the combinations used by Davidson in the experiments which he followed in England. Three combinations of hosts which are similar to those used by Davidson are indicated in the table. However, he used *Euonymus europæus* and *Rumex sanguineus*. In one unsuccessful case which I have listed, transfers were made successfully to another known host. Thus aphids from stock on *Daucus carota*, when transferred to *Chenopodium album*, did not colonize the second host, but did colonize *Rumex crispus*. Since repeated transfers were successfully made between *Rumex crispus* and *Chenopodium album*, the failure mentioned did not throw out *Daucus carota* as a host plant of *Aphis rumicis*.

Since the aphids collected in the field from the various host plants and those used in these tests do not differ from each other by

TABLE VI *Aphis rumicis*—1923—Bustleton, Pa.

Date	Temp.		First-born Generation Series											
	Max.	Min.	1	1-1	1-2	1-3						2	2-1	2-2
April 4	70	54	b*											
5	74	56	x											
6	66	42	x											
7	69	36	x											
8	62	40	x											
9	50	28	x											
10	56	30	x											
11	64	35	x											
12	61	38	x											
13	56	42	x									b#		
14	42	34	x									x		
15	43	32	x									x		
16	58	34	3	b								x		
17	55	35	3	x								x		
18	53	31	x	x								x		
19	59	32	x	x								x		
20	82	34	x	x								x		
21	84	47	x	x								x		
22	72	58	x	x								x		
23	68	53	x	x								x		
24	60	37	x	x								x		
25	66	44	x	x								3	b	
26	68	56	x	x								x	x	
27	73	63	3	b								x	x	
28	75	47	2	x								x	x	
29	64	53		x								x	x	
30	61	44		x								x	x	
May 1	66	36		x								x	x	
2	70	39		x								x	x	
3	71	41		x								x	x	
4	81	41		x								x	x	
5	78	43		x								x	x	
6	74	49		x								x	x	
7	77	48		x								x	x	
8	75	48		x								5	b	
9	66	40		x									x	
10	56	36		3	b								x	
11	67	32		6	x								x	
12	76	55		5	x								x	
13	72	55		4	x								x	
14	73	45		e	x								x	

b—born d—died e—incomplete record x—dev. period

* Stem mother from eggs on *Chenopodium album*, all generations reared on *Rumex crispus*.# Stem mother from eggs on *Viburnum opulus*, generations 2 to 15 reared on *Rumex crispus*, 18 to 20 on *Chenopodium album*.

TABLE VI (Cont.) *Aphis rumicis*—1923—Bustleton, Pa.

Date	Temp.		First-born Generation Series									
	Max.	Min.	1-3	1-4	1-5	1-6	1-7	2-2	2-3	2-4	2-5	2-6
May 15	16	45	x					x				
16	77	58	x					x				
17	77	53	x					x				
18	71	48	x					x				
19	75	54	x					x				
20	76	49	x					x				
21	73	54	x					x				
22	70	56	x					x				
23	72	54	x					x				
24	72	56	x					5	b			
25	80	56	2	b				6	x			
26	83	62	8	x				2	x			
27	85	60	8	x				11	x			
28	80	54	5	x				4	x			
29	88	56	2	x				10	x			
30	80	57	3	x				5	x			
31	75	56	3	x				5	x			
June 1	80	49	2	x				6	x			
2	93	59	4	x				9	6	b		
3	89	62	5	11	b			8	11	x		
4	87	61	9	10	x			5	6	x		
5	87	70	4	8	x			10	7	x		
6	88	75	0	8	x			3	e	x		
7	81	68	d	11	x			6		x		
8	78	60		2	x			2		x		
9	69	55		2	x			2		x		
10	78	51		6	x			2		4	b	
11	76	57		8	2	b		0		7	x	
12	80	54		1	1	x		0		2	x	
13	70	56		3	3	x		0		2	x	
14	86	60		2	2	x		0		4	x	
15	82	59		7	6	x		1		5	x	
16	81	59		3	0	x		0		2	x	
17	88	60		4	9	x		d		3	x	
18	91	54		2	8	x				3	2	b
19	90	57		1	1	x				1d	2	x
20	100	66		2	5	1	b				6	x
21	98	80		0	4	2	x				6	x
22	92	69		0	4	3	x				0	x
23	87	60		0	4	2	x				7	x
24	99	80		d	4	4	x				e	x

TABLE VI (Cont.) *Aphis rumicis*—1923—Bustleton, Pa.

Date	Temp.		First-born Generation Series														Last-born Gen. Series	
	Max.	Min.	1-5	1-6	1-7	1-8	1-9	1-10	1-11	1-12	2-6	2-7	2-8	2-9	2-10	2-11	1-8a	1-8b
June 25	96	67	2	4	x						x							
26	91	79	4	5	x						x							
27	87	67	0	d	x						x							
28	87	64	2		x						4	b						
29	75	59	3		2	b					3	x						
30	81	59	0		3	x					2	x						
July 1	84	49	0		3	x					2	x						
2	83	54	0		3	x					3	x						
3	76	56	0		2	x					1	x						
4	85	61	0		4	x					0	x						
5	92	60	0		2	x					3	x						
6	86	68	0		2	x					1	x						
7	85	59	0		6	4	b				1	1	b					
8	84	55	d		1	1	x				1e	3	x					
9	83	59			3	2	x				3	5	x					
10	91	66			3	3	x				5	6	x					
11	88	70			3	11	x				6	x						
12	87	70			d	8	x				4	x						
13	89	65				3	x				8	x						
14	86	60				4d	2	b			5	x					b	
15	82	67					5	x			5	2	3	b			x	
16	88	67					2	x			6	3	x	x			x	
17	87	62					5	x			2	2	2	x			x	
18	90	63					0	x			4	2	x	x			x	
19	85	57					0	x			3	3	2	x			x	
20	90	55					1	x			1	1	x	x			1	
21	97	67					1	x			2d	4	x	x			10	
22	91	67					0	2	b			5	x	x			5	
23	81	58					d	7	x			5	x	x			6	
24	77	57						2	x			2	x	x			2	
25	83	65						2	x			3	x	x			3	
26	82	58						4	x			2	1	b			4	
27	82	55						3	x			2	2	x			3	
28	80	65						4	x			3	4	x			3	b
29	89	68						4	x			1	1	x			3	x
30	81	67						d	1	b		1d	1	x			d	x
31	67	62							1	x			1	x				x
Aug. 1	70	60							3	x			2	x				x
2	84	62							2	x			0	x				x
3	89	68							1	x			2	x				x
4	90	70							2d	x			1	2	b			x
5	88	72								x			6	4				x

TABLE VI (Cont.) *Aphis rumicis*—1923—Bustleton, Pa.

Date	Temp.		First-born Generation Series												Last-born Gen. Series			
	Max.	Min.	1-12	1-13	1-14	1-15	1-16	2-9	2-10	2-11	2-12	2-13	2-14	2-15	1-8b	1-8c	1-8d	1-8e
Aug. 6	90	65	x					6	5	x					5			
7	89	67	1	b				3	5	x					5			
8	89	72	1	x				1	3	x					1	b		
9	84	76	2	d				d	2	x					d	x		
10	84	69	1	b					3	x						x		
11	81	75	d	x					0	x						x		
12	84	70		x					2	3	b					x		
13	81	68		x					d	2	x					x		
14	80	62		x						2	x					x		
15	88	66		x						4	x					x		
16	77	57		x						4	x					1		
17	71	59		x						2	x					2	b	
18	83	62		x						3	x					d	x	
19	83	53		2	b					0	x						x	
20	81	62		4	d					d	x						x	
21	86	52		1						3	b						x	
22	82	53		1	b					2	x						x	
23	72	56		d	x					2	x						x	
24	78	53			x					0	x						x	
25	81	60			x					1	x						x	
26	82	62			x					2	x						x	
27	81	54			x					2	x						x	
28	84	64			x					e	x						x	
29	81	64			x						x						x	
30	85	61			x						x					1d	b	
31	84	56		2		b					4	b					x	
Sept. 1	83	59		4	x							3	x				x	
2	87	67		3	x							3	x				x	
3	85	61		5	x							3	x				x	
4	91	68		1	x							4	x				x	
5	80	64		1	x							4	x				x	
6	81	61		2	x							3	x				x	
7	83	62		2	x							1	x				5	
8	82	66		1	x							3	x				2	
9	80	57		0	x							3	x				4	
10	75	62		0	2	b						3	2	b			4	
11	77	62		0	2	x						1	3	x			2	
12	79	57		0	2	x						2	2	x			2	
13	77	58		0	2	x						3	0	x			2	
14	69	58		d	2	x						0	1	x			3	
15	68	42			2	x						1	2	x			3	
16	70	50			3	x						d	1	x			2	

TABLE VI (Cont.) *Aphis rumicis*—1923—Bustleton, Pa.

Date	Temp.		First-born Generation Series										Last-born Gen. Series	
	Max	Min.	1-15	1-16	1-17	1-18	1-19	2-14	2-15	2-16	2-17	2-18		
Sept. 17	72	40	2	x				0	x					
18	74	38	0	x				0	x					
19	82	60	2	x				2	x					
20	80	64	6	x				4	x					
21	73	67	3	x				1	4	b				b
22	73	66	2	2	b			2	4	x				x
23	80	66	3	3	x			2	4	x				x
24	83	65	5	2	x			2	5	x				x
25	85	60	4	1	x			0	1	x				x
26	79	58	1	0	x			1	d	x				x
27	78	61	3	2	x			4		x				x
28	80	58	1	1	x			3		x		b		x
29	81	58	4	1	x			0	1	1				4
30	68	50	0	2	x			1	d	2	x			2
Oct. 1	67	44	d	0	x			d		1	x			0
2	72	52		d	x					2	x			2
3	68	45			x					1	x			1
4	73	44			x					2	x			2
5	62	37			2	b				3	x			2
6	62	40			0	x				0	x			3
7	63	32			0	x				0	x			0
8	64	34			0	x				1	x			0
9	68	40			0	x				0	x			3
10	70	38			0	x				1	x			2
11	67	45			0	x				0	x			4
12	73	43			4	x				0	x			2
13	70	50			2	x				0	x			2
14	77	55			0	x				0		b		3
15	72	59			3	x				0	4	x		6
16	73	54			2	x				0	1	x		4
17	70	41			1	x				0	1	x		3
18	74	43			1	x				0	1	x		2
19	66	49			2	x				2	1	x		2
20	66	53			0	x				2		e		1
21	64	50			0	3	b			1		x		5
22	60	38			2	1	x			1		x		2
23	50	43			0	0	x			0		x		0
24	58	43			2	0	x			0		x		0
25	58	40			2	1	x			0		x		2
26	54	44			0	0	x			0		x		2
27	62	37			0	1	x			1		x		0
28	60	31			0	0	x			1		x		1

TABLE VI (Cont.) *Aphis rumicis*—1923—Bustleton, Pa.

Date	Temp.		First-born Generation Series										Last-born Gen. Series	
	Max	Min.	1-17	1-18	1-19		2-16	2-17	2-18	2-19				
Oct. 29	67	48	0	2	x		4		x				1	
30	72	46	1	3	x		3		x				4	
31	65	42	0	2	x		0		x				2	b
Nov. 1	48	30	0	0	x		d		x				0	x
2	53	27	0	0	x				x				0	x
3	60	26	0	0	x				2	b			d	x
4	63	27	1	1	x				1	x				x
5	63	53	0	0	x				1	x				x
6	57	46	1	3	x				1	x				x
7	50	43	1	d	x				1	x				x
8	47	37	0		x				1	x				x
9	44	26	0		x				0	x				x
10	51	24	0		x				0	x				x
11	58	31	1		x				1	x				x
12	51	39	1		x				1	x				x
13	53	34	0		x				1	x				x
14	60	37	0		x				0	x				x
15	49	35	0		x				1	x				x
16	48	42	0		x				0	x				x
17	49	40	0		x				1	x				x
18	51	39	0		x				0	x				x
19	41	30	1		x				1	x				x
20	48	20	1		x				0	x				x

All experiments terminated Nov. 20.

On Nov. 20:

1-17 Apterous viviparous female alive.

1-19 Pupæ of males with wing pads.

2-18 Apterous viviparous female alive.

2-19 Practically mature apterous viviparous female.

1-8g Nymphs in 3rd and 4th instar.

First hard frost Nov. 6-10.

variations greater than those found in a collection of individuals reared from known stock on one host such as *Rumex crispus*, I concluded that these belong to the one species, *Aphis rumicis* Linn. The question as to the possibility of physiological species being present on different hosts has been suggested, but my experiments seem to indicate, as did Davidson's that such is not the case.* In the cage experiments, sexuparae from *Chenopodium* migrated to *Euonymus* and oviparae developed and laid eggs on the *Euonymus* while eggs were also secured on *Chenopodium album* from the same strain. Strains from *Chenopodium album* laid eggs on *Viburnum opulus* and those from *Maclura pomifera* produced eggs on *Rumex crispus*.

NUMBER OF GENERATIONS

During the seasons of 1920-21-22-23, eight first-born generation series were conducted. The data obtained from two series of 1923 are presented in Table VI. Series 1 was started by collecting eggs on *Chenopodium album* which had remained out of doors all winter. These eggs, on small bits of the dried stems, were brought into the insectary March 27 and placed on the soil at the base of potted plants of *Rumex crispus*. The first eggs hatched on April 4 and the young began feeding on the leaves of the *Rumex*. The experiments were transferred to the insectary on April 27 and all succeeding generations were reared out of doors. All generations of Series 1 were reared on *Rumex crispus* and *Rumex obtusifolius*. From April 4 to Nov. 20, the date the experiments were closed, twenty first-born generations occurred in this series. The series closed with a male in the last nymphal instar. During the summer, a total of six days were lost, three days between generations 12 and 13 and three between 13 and 14.

Series 2 was started with a mature stem mother taken from *Viburnum opulus* on April 27. It is probable that this individual

*Additional transfer experiments conducted during the spring of 1924, confirm my contention that physiological strains, confined to certain host plants, are not demonstrable. Stem mothers in the first instar from eggs on *Viburnum opulus* were transferred to *Rumex obtusifolius*. These aphids matured normally on this food plant and individuals of the third viviparous generation were present when the experiment closed. Stem mothers in the first instar taken on *Rumex obtusifolius* in the field, contemporaneous with hatching of eggs on *Viburnum*, matured and founded colonies on *Rumex* in the insectary. Progeny from this stem mother on *Rumex* were successfully transferred to *Viburnum opulus*, *Euonymus alatus*, *Celastrus scandens*, *Maclura pomifera*, and *Philadelphus coronarius*.

hatched from the egg about April 10 and matured April 25. First-born young which were two days old, comprising the second generation, were taken with the stem mother. Series 2 closed on Nov. 20 with a male nymph of 4th instar. This aphid was an individual of the twentieth first-born generation of an unbroken series. The first individual in Series 2 matured on *Viburnum*. Generations 2 to 15 inclusive were reared on *Rumex crispus*. Generations 16 to 20 inclusive were reared on *Chenopodium album*.

The remaining six series of the total of eight were incomplete in that each was started with a winged migrant taken from one of the summer food plants in the field. The possible number of generations which might obtain in the case of each series has been determined by combining the number obtained in each series with the probable number of generations occurring before the date the series started. The probable previous number of generations was obtained by a comparison of the date of starting with the number of the generation maturing on the nearest date to this in series 2 for 1923. The summary of these data will be found in Table VII. It will be noted that from the eight separate series, one had a possible 17 first-born generations, two had 18 first-born generations, two 19 generations, two had 20 generations, and one had 21 generations, the model number of the eight series being 19.

A last-born of last-born series was started on July 14 from the individual born in generation 9 of series 1. The series was closed on Nov. 20 with the 7 generations. During this same time 11 first-

TABLE VII

Date of Experiment	No. Generations	Possible No. of Generations
1920		
August 19 to November 12	8	21
1921		
May 21 to November 11	15	18
1922		
May 30 to November 10	13	17
June 30 to November 10	12	19
July 14 to November 10	10	19
1923		
April 4 to November 20	20	
April 10 to November 20	20	
June 2 to November 20	14	18

TABLE VIII—SUMMARY OF FIRST-BORN GENERATION EXPERIMENTS

Exp. No.	Date of Birth	Date of First Young	Age at Birth of First Young	Date of Last Young	Period-days	Total Young	Average Young per Day	Maximum Young in one Day	Period after Last Young	Date of Death or Disappearance	Total Length of Life
1	1923	April 4	12	?	2	6	3.0	3	?	?	14*
1-1	April 16	April 27	11	?	2	5	2.3	3	?	?	12*
1-2	April 27	May 10	13	May 13	4	18	4.5	6	1	May 14	17*
1-3	May 10	May 25	15	June 5	12	55	4.5	9	2	June 7	28
1-4	May 25	June 3	9	June 20	18	91	5.	11	4	June 24	30
1-5	June 3	June 11	8	June 29	19	64	3.3	9	9	July 8	35
1-6	June 11	June 20	9	June 26	7	21	3.0	5	1	July 27	16
1-7	June 20	June 29	9	July 11	13	37	2.8	6	1	July 12	22
1-8	June 29	July 7	8	July 14	8	36	4.5	11	0	July 14	16
1-9	July 7	July 14	7	July 21	8	16	2.0	5	2	July 23	16
1-10	July 14	July 22	8	July 29	8	28	3.5	7	1	July 30	16
1-11	July 22	July 30	8	Aug. 4	6	10	1.6	3	0	Aug. 4	14
1-12	July 30	Aug. 7	8	Aug. 10	4	5	1.2	2	1	Aug. 11	12
1-13	Aug. 10	Aug. 19	9	Aug. 22	4	8	2.0	4	1	Aug. 23	13
1-14	Aug. 22	Aug. 31	9	Sept. 8	9	21	2.3	5	6	Sept. 14	23
1-15	Aug. 31	Sept. 10	10	Sept. 29	20	52	2.6	6	2	Oct. 1	31
1-16	Sept. 10	Sept. 22	12	Sept. 30	9	14	1.5	3	2	Oct. 2	22
1-17	Sept. 22	Oct. 5	13	Nov. 20	47	32	.7	4	0	Nov. 20	60†
1-18	Oct. 5	Oct. 21	16	Nov. 6	17	17	1.0	3	1	Nov. 7	33
1-19	Oct. 21	Nov. 20	30								†

2	April 10	April 25	15	?	1	3		3	?	?	?	?
2-1	April 25	May 8	13	June 15	1	5		5	?	?	?	?
2-2	May 8	May 24	16	June 5	23	105	4.5	11	2	June 17	40	40
2-3	May 24	June 2	9	June 19	4	30	7.5	11	1	June 6	13*	13*
2-4	June 2	June 10	8	June 23	10	33	3.3	7	0	June 19	18	18
2-5	June 10	June 18	8	June 23	6	23	3.8	7	1	June 24	14*	14*
2-6	June 18	June 28	10	July 8	11	21	2.0	4	0	July 8	21*	21*
2-7	June 28	July 7	9	July 21	15	59	3.9	8	0	July 21	24	24
2-8	July 7	July 15	8	July 30	16	42	2.6	5	0	July 30	24	24
2-9	July 15	July 26	11	Aug. 8	14	32	2.2	6	1	Aug. 9	25	25
2-10	July 26	Aug. 4	9	Aug. 12	9	26	2.8	5	1	Aug. 13	18	18
2-11	Aug. 4	Aug. 12	8	Aug. 18	7	20	2.8	4	2	Aug. 20	16	16
2-12	Aug. 12	Aug. 21	8	Aug. 27	7	12	1.7	3	1	Aug. 28	16*	16*
2-13	Aug. 21	Aug. 31	10	Sept. 15	16	41	2.5	4	1	Sept. 16	26	26
2-14	Aug. 31	Sept. 10	10	Sept. 30	21	33	1.5	4	1	Sept. 1	31	31
2-15	Sept. 10	Sept. 21	11	Sept. 25	5	18	3.6	5	1	Sept. 26	16	16
2-16	Sept. 21	Sept. 29	8	Oct. 30	32	29	.9	4	2	Nov. 1	41	41
2-17	Sept. 29	Oct. 14	15	Oct. 19	6	10	1.6	4	1	Oct. 20	23*	23*
2-18	Oct. 14	Nov. 3	20	Nov. 19	17	13	.7	2	1	Nov. 20	38†	38†
2-19	Nov. 3	Nov. 20	17									

*Incomplete record.

†Terminated Nov. 20

born generations had occurred in Series 1. From this known ratio between the number of first-born and last-born generations, we may conclude that *Aphis rumicis* would have a minimum of 12 generations for the entire season.

MOLTING

Aphis rumicis, like most other aphids, molts four times or passes through four nymphal instars before it reaches maturity. My observations, covering four consecutive years, indicate that the general trend is for the individual to molt between daylight and 9:00 A. M. This is not invariable, since some individuals molted later during the day, but never at night. The following figures represent data obtained from experiments covering the months of June, August and September. The length of the first instar in 40 cases ranged from 1 day to 3 days with a mean period of 2 days. The period between the first molt and second molt varied from 2 days to 4 days with a mean of 2 days in 27 cases. The mean period for the third instar was 2 days for 27 cases with a range from 1 day to 6 days. The mean length of time spent in the fourth instar was 2 days in 21 cases with a range of 1 day to 6 days. The length of time elapsing from the date of the last molt to the birth of the first young varied from 0 days to 9 days with a mean for 14 cases of 1 day. All individuals in these experiments which reached maturity were apterous females. The mean length of the second, third and fourth instars for September was 3 days. This is to be correlated with the data in Table VIII which shows that the generations in the fall required a greater length of time to reach maturity than did those which matured in mid-summer.

AGE AT WHICH FEMALES REPRODUCE

The length of time which was consumed by viviparous females from birth until they gave birth to their first progeny varied according to the time of year in which they appeared. This period ranged from seven days in July or August, to twenty days in late October and early November. The mean length of the developmental period was 10.5 days for all seasons of the year. These figures represent 119 individuals reared in 1920, 1921, 1922, and 1923. It will be noted that this difference in the length of the developmental period is seasonal by referring to Table IX. In this table the mean length of the developmental period has been determined for individuals grouped according to date of birth.

The limits of these several groupings were arbitrarily selected and all individuals born or developing within limits of any one group were classed together. The cases represent records covering the four seasons from 1920 to 1923.

TABLE IX

<i>Period of Birth</i>	<i>Dev. Period</i>	<i>No. of Individuals</i>
April 4 to June 15	11.6	16 cases
June 15 to August 20	9.0	37 cases
August 20 to November 4	11.6	43 cases

It will be seen that the individuals born from April 4 to June 15 had a mean developmental period of 11.6 days; those born between June 15 and August 20 had a mean developmental period of 9.0 days; those born between August 20 and November 4 had a mean developmental period of 11.6 days.

The data which are given above for *Aphis rumicis* agree very closely with information obtained in the same laboratory on *Myzus persicae*. The average age of 65 mothers of *Myzus persicae* was found to be 10.2 days and the seasonal range was practically the same, i.e. 11 days in spring and fall, and 9 days in summer.

This variation in the age of females of *Aphis rumicis* at the birth of the first progeny is illustrated in digrammatic form by Plate I, B. In this figure the lower solid line shows the variation in the age of females at birth of first young for first born generations in 1923. The upper dotted line represents the mean temperatures which obtain for each of these developmental periods for the several generations. In general, the trend shows that in the spring and fall when temperatures are low the developmental period is fairly long, while in the summer when mean temperatures are higher the insects mature in much shorter time.

REPRODUCTION

The shortest period of reproduction, for a single female under observation in any one of the four seasons, was 3 days. Several cases were recorded in which the period extended over 4 days in August and some in which the period was 5 days in July. One female, born on Sept. 22, 1923, was bearing young on Nov. 20 when the experiment closed. The reproduction period for this individual covered 47 days. Other individuals, having a reproduction period of 25 to 32 days were common in late September,

October, and November. The average length of reproductive period for 79 females was 12.6 days. I found that the total number of young produced by a female during her lifetime ranged from 2 to 105 aphids with an average of 24.6 young per mother for 76 individuals. Only those individuals were considered in securing this average which died from natural causes at a definitely determined date. The maximum number of young borne by one mother in a single day was 13.. This mother was feeding on spinach during May. Four other individuals each produced a maximum of 11 young in one day. The average number of young born to one female in a day was 2.1, average obtained from 119 cases.

LONGEVITY

The length of life of females after the birth of the last young varied considerably averaging 2.2 days for 78 cases. Six females died on the same day on which they gave birth to the last young. One female lived 12 days after the birth of the last young and two individuals lived 9 days. The total length of life of individual females in the generation experiments ranged from 10 days to 48 days. The average length of life for 76 females was 23.3 days. It may be noted that the average length of life of *Myzus persicae* was found to be 23.5 days in work done on that species at the same laboratory.

THE OCCURRENCE OF ALATE FORMS

In general the winged viviparous females of *Aphis rumicis* may be grouped as spring migrants, migrants appearing during the summer generations, and fall migrants. The appearance of the spring and fall migrants is fairly constant and may be looked for (within a certain range) at about the same time each year. The appearance of summer migrants, on the other hand, does not seem to be so definitely defined and may or may not appear in any given summer generation. In my rearing cages considerable numbers of the daughters of stem mothers from *Viburnum* series No. 2 became winged adults on May 8 to 11, 1923. On May 8 of the same year, the first winged female was taken on the flower spikes of *Rumex crispus* in the field. In the same experiment, 90% of all grand-daughters of stem mothers or the daughters of the wingless females of the second generation became winged viviparae on May 23. The first winged forms to appear in the series No. 1 on *Rumex*, from stem mothers hatched from eggs on *Chenopodium* stems and reared

for the first two generations in the laboratory, were of the 4th generation, i.e., were great grand daughters of the stem mothers. These individuals matured May 24 on *Rumex crispus* with 92% winged. Thus, winged forms from the *Viburnum* strain appeared in predominating numbers in the 3d generation and in the *Chenopodium* strain on *Rumex* in the 4th generation, but they matured simultaneously in the insectary. The field collections for four years also indicate that the predominating spring migration takes place about the third week in May, and that the earlier migrants noted in early May, were comparatively of much smaller numbers. Practically all individuals which were taken were migrants on *Viburnum* on May 21, 1920 and again on May 21, 1922. Migrants were noted as leaving *Euonymus atropurpureus* on May 22, 1922. The first record of migrants and young on a summer host plant, *Rumex crispus*, in 1922, was taken on May 21. Infestation by migrants and young on lima beans was noted at Bustleton, Penn., on May 31, 1920. Light infestation, started by migrants on *Arctium lappa*, was noted at Iowa City, Iowa, on May 22, 1922. First infestations on *Chenopodium album* in the spring were on May 31, 1922 and on June 6, 1923. It will be seen that these typical records, and many others of a similar nature, in my files, show that an obvious relationship exists between the aphids migrating from *Viburnum*, *Euonymus* and other plants in the spring and the migrants appearing at the same time on *Chenopodium*, *Rumex* and *Arctium lappa*.

Neither the records made on generation experiments nor notes taken at time field collections were made, serve to clarify the problem as to what actually induces the appearance of winged forms during the summer. In my rearing experiments, these winged forms appeared from time to time, but in no definite generation or time of the season. No correlation was found between date of appearance and host plant or possible differences in materials in plant sap. I found that in Series 1 on *Rumex crispus* all young matured into apterous viviparæ from the 5th generation to the 12th generation. In the 12th generation, maturing on July 31, 1923, 3 out of 9 individuals or 33% were winged. In Series 2 on *Rumex crispus*, individuals of the 4th and 5th generations matured into wingless females, but 25% of the adults comprising generation six in this series matured into winged viviparæ on June 18, 1923. In Series 3, generation 6 (10th in line), on *Chenopodium*

album, 4 out of 8 individuals became winged viviparæ on July 24, 1923. In this same series on *Chenopodium album*, winged individuals appeared on Sept. 14, 1923. At this time, all forms maturing in Series 1 and 2 were wingless. In this grouping, the winged individuals appearing from June 1 to Sept. 15-20 have been considered as summer migrants. By referring to collection records in the food plant list it will be noted that winged viviparæ were taken during each of the months from June to October on a wide range of host plants. I feel that the appearance of the fall migrants or winged sexuparæ is more or less linked up in some way with temperature since they appear consistently in regions of the United States with decline of mean temperature in the fall of the year, but do not appear in California where fall does not bring such a low temperature. It may be as Davidson (18) suggests, that it is attributable to some combination of internal factors, but the direct stimulus would seem to be climatic in nature. In my experiments winged sexuparæ matured Oct. 23, 1921, on *Chenopodium album*, on Oct. 27, 1923, in Series 3 on *Chenopodium album*, in the 18th first born generation, and in Series 1 on Oct. 20-25, 1923, on *Rumex crispus* all but 8 out of 9 became winged sexuparæ. In the field, collections were made of winged sexuparæ maturing on summer hosts from Oct. 6 to Oct. 31 and alighting and bearing young on winter hosts during the same period.

Recent experimental work on this particular problem has resulted in evidence which is largely contradictory in nature. Mason (55) found that changes of environment with which he worked, i.e., effect of injury to food plants, crowding, and the addition of chemical solutions to food plants, had no bearing on production of winged forms in the first generation. He concluded that the young aphid, when born, has its adult condition as regards presence or absence of wings already determined and that there is no positive evidence in favor of such influences even to the third generation. Uichanco (94) failed to obtain fall migrants of *Aphis rumicis* when forms were reared in the greenhouse under optimum temperature conditions. Wadley (96) concluded that the factors of nutrition, parentage, and temperature were all important in causing appearance of winged forms, but that these factors must be applied before the second molt.

APPEARANCE OF SEXES

It is only within recent years that any winter hosts, other than *Euonymus europæus* and *Viburnum opulus* have been known to be selected by *Aphis rumicis*. Theobald (88) reported finding the eggs on petioles of *Rumex crispus*, but, so far as I can learn, did not observe the hatching of these eggs and founding of the colony by the stem mother the following season. Davidson (17) reported the rearing of sexes on broad beans and *Euonymus europæus* under controlled conditions and cites records of sexual females ovipositing on sugar-beet (Gaumont) (1913) and on haricot beans (Malaquin and Moitre) (1914). Davidson made this further observation: "The spindle-tree is undoubtedly a winter host of *Aphis rumicis*, but considering the local distribution of *Euonymus* in Britain it is highly probable that there are other winter hosts." I was so forcibly impressed by the same idea when I began these studies that I made very careful collections from shrubs and summer hosts of *A. rumicis* in order to ascertain these other possible hosts. Conclusions as to the names, which should be included as winter hosts are based on careful determinations of field collections, transfer tests, and copulation experiments. I have conducted many tests in which I selected a male taken from a certain host plant and placed it on a plant upon which an oviparous female was feeding. In many cases this experiment was reversed and the oviparous female from a certain host was crossed with a male from a different host. Although I realize that results of such copulation experiments are not of themselves entirely conclusive it seems that such information is not only interesting, but desirable when it is correlated with results of transfers made at other times during the year. In some of the cases the individuals which were paired were taken from different host plants. In other cases these pairings were made between males and oviparous females from the same host plant. I have been unable to find in literature any mention of similar experiments with this species. The cases in which successful copulation was effected are listed in Table X. In some cases the male was transferred to the plant upon which the oviparous female was feeding by means of a small brush, and the transfer in this case was somewhat aided. In other cases the plant upon which the male was feeding was placed inside a large cage together with the plant upon which oviparæ were feeding. In this case the males migrated to the host of the oviparæ themselves. Only cases in which actual copulation was effected are listed.

TABLE X—COPULATION TESTS

Date	Host of Male	Host of Female	No. of cases
Oct. 18	<i>Chenopodium album</i>	<i>Viburnum opulus</i>	1
Oct. 20	" "	" "	2
Oct. 25	" "	" "	6
Oct. 25	" "	" "	6
Oct. 15	" "	<i>Euonymus alatus</i>	1
Oct. 23	" "	<i>Chenopodium album</i>	6
Oct. 28	" "	" "	4
Oct. 23	<i>Arctium lappa</i>	<i>Rumex crispus</i>	2
Oct. 28	" "	" "	1
Oct. 28	" "	<i>Arctium lappa</i>	5
Nov. 29	<i>Rumex crispus</i>	<i>Rumex crispus</i>	several
Oct. 23	<i>Viburnum opulus</i>	<i>Viburnum opulus</i>	4
Oct. 30	" "	<i>Euonymus alatus</i>	2
Oct. 29	<i>Euonymus alatus</i>	" "	2
Oct. 30	" "	<i>Viburnum opulus</i>	1
Oct. 23	<i>Maclura pomifera</i>	<i>Maclura pomifera</i>	several
Oct. 24	" "	<i>Viburnum opulus</i>	1

In the field, during October, I have taken males and oviparous females in copulation on *Arctium lappa*, *Chenopodium album*, *Viburnum opulus*, *Euonymus alatus*, *Maclura pomifera*, *Celastrus scandens*, and *Philadelphus coronarius*. Sexes were also taken during October from *Rumex crispus*, *Hydrangea paniculata* and *Calycanthus fertilis* which agreed morphologically with the same forms taken in copulation on the other hosts. It thus appears as Davidson has suggested that the number of winter hosts of *Aphis rumicis* is quite numerous.

In America, the winter hosts which have been recorded, in addition to *Euonymus* and *Viburnum*, include *Celastrus scandens* and *Hedera* in Conn., Patch (10) and *Philadelphus coronarius* in New York, Ohlendorf (62). Ohlendorf substantiated records of *Philadelphus*, *Viburnum* and *Euonymus* by transfers between these hosts.

I found that the migrants, which are the progeny of apterous viviparæ on summer hosts, were the winged sexuparæ which give birth to oviparous females. These oviparæ are born and develop either on some of the herbaceous hosts such as *Rumex obtusifolius*, *Rumex crispus*, *Chenopodium album* and *Arctium lappa* or on the woody shrubs such as *Euonymus atropurpureus*, *Viburnum opulus*, *Philadelphus coronarius*, *Hydrangea paniculata*, *Celastrus scandens*, *Maclura pomifera*, etc. The males are the progeny of apterous sexuparæ and develop on the so-called summer hosts. The offspring of these apterous sexuparæ are not always males exclu-

sively. In my experiments, males, migrants or winged sexuparæ, and apterous sexuparæ were born by the same mother. The sexuparæ, males, and oviparous females develop during October and early November in Iowa and Pennsylvania.

It should be noted that Swain (84) did not take the true sexes of *Aphis rumicis* in California but found it developing parthenogenetically throughout the year on its summer hosts. I reared this species in the greenhouse on *Rumex crispus* from Sept. 1921 to June 1922. At no time did true sexes appear in these cages. Davidson, (17) under similar conditions in England, obtained a certain proportion of sexual forms in five succeeding generations.

COPULATION AND EGG-LAYING

A male may copulate with more than one female. A male was observed to copulate with two separate females on the same plant. An interval of fifteen minutes to one-half hour elapsed between the times of copulation in three different cases under observation. When the male approached, the female elevated the tip of the abdomen and moved the hind legs vigorously about in the air. In several cases after mounting the female, the male was observed attempting to insert the penis at the head of the female. Failing in this, the male turned slowly about and successfully completed the act.

A series of experiments was conducted to secure data on the number of eggs laid by a single female. At the time the experiments closed on November 21, all females still living were dissected and the number of ova still within the body were counted, (Table X). A series of ten grown females reared on *Chenopodium album* was dissected on Nov. 12 and the number of ova was counted. The counts were as follows: 1, 8 ova; 2, 7 ova; 3, 6 ova; 4, 6 ova; 5, 5 ova; 6, 8 ova; 7, 7 ova; 8, 5 ova; 9, 5 ova; 10, 6 ova. The mean in this case is 6.3 ova per female.

From my observations of cage experiments, the oviparous female does not deposit all of her eggs at one time, but the period of egg deposition is extended over a period of one to two weeks. The eggs when first laid are olive green in color. The coat hardens and within a day becomes shiny-black. Eggs which are laid upon the woody winter hosts such as *Viburnum opulus*, etc., are usually placed in the axils between the bud and the stem. On *Rumex crispus* and *Rumex obtusifolius* they are fastened by the mucilaginous secretion to the underside of the leaf, usually along the

petiole or mid vein. On *Chenopodium album*, the eggs may be found tucked into old scars or breaks in the stem, in the axils formed by the side branches with the main stem, and even glued up and down the main stem unprotected.

TABLE XI

Food Plant of Ovip. Female	Exp. started	Copulation with male	No. of eggs Nov. 21	Notes
<i>Rumex obtusifolius</i>	Oct. 22	Oct. 25	5	dead ♀
<i>Rumex obtusifolius</i>	Oct. 25	Oct. 31	1	dead ♀
<i>Chenopodium album</i>	Oct. 25	Oct. 25	2	dead ♀
<i>Chenopodium album</i>	Oct. 25	Oct. 25	8	3 in ♀
<i>Rumex crispus</i>	Oct. 25	Oct. 25	2	0 in ♀
<i>Chenopodium album</i>	Oct. 31	Oct. 31	3	2 in ♀
<i>Chenopodium album</i>	Oct. 31	Nov. 2	4	1 in ♀

Oviparous females taken from *Maclura pomifera* while in the fourth instar, were transferred to *Rumex obtusifolius* Oct. 22. These matured on *Rumex* and deposited eggs. Oviparous females taken from *Chenopodium album* Oct. 16, when transferred to *Euonymus atropurpureus*, matured and oviposited on *Euonymus*.

The question arises as to whether development of oviparae on herbaceous plants and consequent egg deposition on the same is accidental in some cases, the chance result of migrants alighting on these plants. Although this may have been the case with *Aphis rumicis* at some previous stage in its development, I have come to believe that here in the Eastern and Central United States, at least, it is an adaptation which helps to insure perpetuation of the species. *Rumex crispus* and *Rumex obtusifolius* are perennials and some of the rosettes of leaves never entirely die, but survive the winter. Other new leaves are shot out at the earliest advent of spring. Aphids hatching in April, from eggs deposited on either of these plants, find the food necessary for development. I have taken stem mothers on *Rumex crispus* and *Rumex obtusifolius* in the spring at the same time they were found on *Euonymus* and *Viburnum*. In the case of aphids hatching from eggs on *Chenopodium album*, it is different for this is an annual. However, it must be remembered that *Chenopodium album* is invariably found in the same habitat with these two species of *Rumex*. It is then probable that the aphids upon hatching from eggs on *Chenopodium album* crawl down the dead stem and seek nearby *Rumex* plants. Young *Chenopodium album* plants are just sprouting at the time the eggs hatch. This supposition is strengthened by the fact that this very pro-

cedure took place in my experiments, not in one case, but in fourteen cases. I have found no record in the literature of observations showing the hatching of eggs deposited on herbaceous plants.

Dr. Fitch (32) found two newly-deposited eggs on pigweed (*Chenopodium?*) but regarded these as accidental. His notes under heading of *Aphis rumicis* Linn., December, 1870 read: "Where the eggs are laid and how the insect is carried through the winter, has hitherto been a mystery, as Mr. Curtis observes. Upon this important point I am able to shed some light. Upon examining a pigweed infested by these black lice the latter part of October I discovered an egg, slightly adhering to the surface of a dry and crinkled and dead leaf, and another crowded into a crevice in another wrinkled dead leaf, whereby only its end was visible. These no doubt had been newly laid. They were of a dull green color, smooth and shining. Several other infested weeds were examined later in the season, but I was unable to detect any eggs upon them. In November, meeting with a weed that was thronged with pupæ, I transplanted it into a flower pot and brought it in doors to observe whether on maturing, having no other place to lay their eggs, they would not stock this plant with them. But on obtaining wings, they all flew away, without making any deposit of eggs thereon. It was thus evident that the two eggs I found were only placed on the dead leaves by accident, and that they do not lay their eggs upon the plants they inhabit, or at least upon those which decay at the close of the season."

SEASONAL HISTORY

I have outlined, in tabular form, the host plants upon which I have collected *Aphis rumicis* at different periods of the year. This indicates the general occurrence of this aphid as I have found it during the various seasons in Pennsylvania. I found that the eggs on *Viburnum opulus* and *Chenopodium album* hatched about the second week in April. The young stem mothers on *Viburnum opulus* developed on that host while those from eggs on *Chenopodium album* migrated of necessity to *Rumex*. Stem mothers were found developing on *Rumex* in the field during the third week in April. Migrant daughters of stem mothers on *Viburnum opulus* preferred *Rumex* upon which to establish colonies. The migrant granddaughters of stem mothers from *Viburnum* reproduced on *Rumex* and *Arctium*. Migrants from the other winter hosts evidently selected these same plants since colonies were limited to

TABLE XII.—

April	May	June	July
<i>Rumex crispus</i>	<i>Rumex crispus</i>	<i>Rumex crispus</i>	<i>Rumex crispus</i>
<i>Chenopodium</i>		<i>Chenopodium</i>	<i>Chenopodium</i>
<i>album</i>		<i>album</i>	<i>album</i>
<i>Euonymus</i>	<i>Arctium lappa</i>	<i>Arctium lappa</i>	<i>Arctium lappa</i>
<i>atropurpureus</i>			
<i>Viburnum opulus</i>	<i>Viburnum opulus</i>	<i>Viburnum opulus</i>	
	<i>Euonymus</i>	<i>Tropæolum</i>	<i>Tropæolum</i>
	<i>atropurpureus</i>	<i>minus</i>	<i>minus</i>
	<i>Euonymus alatus</i>	<i>Beta vulgaris</i>	
		<i>Amaranthus</i>	<i>Amaranthus</i>
		<i>retroflexus</i>	<i>retroflexus</i>
		<i>Rheum</i>	<i>Rheum</i>
		<i>rhaponticum</i>	<i>rhaponticum</i>
		<i>Spinacia</i>	
		<i>oleracea</i>	
		<i>Phaseolus</i>	<i>Dahlia</i> sp.
		<i>limensis</i>	
		<i>Rumex</i>	
		<i>obtusifolius</i>	
<i>Ova</i>			
<i>Fundatrices</i>	<i>Fundatrices</i>		
<i>Larvæ</i>	<i>Larvæ</i>	<i>Larvæ</i>	<i>Larvæ</i>
	<i>Alate vivip.</i>	<i>Alate vivip.</i>	<i>Alate vivip.</i>
	<i>Apter. vivip.</i>	<i>Apter. vivip.</i>	<i>Apter. vivip.</i>

SEASONAL HISTORY CHART

August	September	October	November
<i>Rumex crispus</i>	<i>Rumex crispus</i>	<i>Rumex crispus</i>	<i>Rumex crispus</i>
<i>Chenopodium album</i>	<i>Chenopodium album</i>	<i>Chenopodium album</i>	<i>Chenopodium album</i>
<i>Arctium lappa</i>	<i>Chenopodium ambrosioides</i>	<i>Arctium lappa</i>	<i>Arctium lappa</i>
<i>Lycopersicon esculentum</i>	<i>Papaver</i> sp.	<i>Capsella bursapastoris</i>	<i>Viburnum opulus</i>
<i>Tropæolum minus</i>	<i>Tropæolum minus</i>	<i>Stellaria media</i>	<i>Euonymus alatus</i>
<i>Daucus carota</i>	<i>Galinsoga parviflora</i>	<i>Galinsoga parviflora</i>	<i>Maclura pomifera</i>
<i>Amaranthus retroflexus</i>	<i>Amaranthus retroflexus</i>	<i>Phaseolus limensis</i>	<i>Celastrus scandens</i>
<i>Rheum rhaponticum</i>	<i>Gladiolus</i> sp.	<i>Viburnum opulus</i>	<i>Euonymus atropurpureus</i>
<i>Spinacia oleracea</i>	<i>Spinacia oleracea</i>	<i>Euonymus atropurpureus</i>	<i>Philadelphus coronarius</i>
<i>Polygonum scandens (dumetorum)</i>	<i>Pisum</i> sp.	<i>Euonymus alatus</i>	<i>Rumex obtusifolius</i>
	<i>Dahlia</i> sp.	<i>Maclura pomifera</i>	
	<i>Phaseolus vulgaris</i>	<i>Celastrus scandens</i>	
	<i>Mirabilis jalapa</i>	<i>Philadelphus coronarius</i>	
	<i>Aster</i> sp.	<i>Hydrangea paniculata</i>	
	<i>Rumex obtusifolius</i>	<i>Calycanthus fertilis</i>	
		<i>Polygonum persicaria</i>	
		<i>Ova</i>	<i>Ova</i>
<i>Larvæ</i>	<i>Larvæ</i>	<i>Larvæ</i>	<i>Larvæ</i>
<i>Alate vivip.</i>	<i>Alate vivip.</i>	<i>Alate vivip.</i>	<i>Alate vivip.</i>
<i>Apter. vivip.</i>	<i>Apter. vivip.</i>	(sexuparæ) <i>Apter. vivip.</i>	(sexuparæ) <i>Apter. vivip.</i>
		(sexuparæ) <i>Oviparæ</i>	(sexuparæ) <i>Oviparæ</i>
		<i>Males</i>	<i>Males</i>

Rumex and *Arctium* during this month. During June, July, August and September, as will be noted, a great variety of hosts may be infested. I was unable to obtain any data which would lead me to believe that migrants from any particular host were selective in their tastes, or in other words, that certain strains of *Aphis rumicis* depending on groups of food plants have been evolved. Theobald (88) has diagrammed a possible dual strain for this species in England. This conclusion was based on his collections and observations in the field.

Fall migrants or sexuparæ, which are the progeny of apterous viviparous females, develop on the summer hosts and in October and early November return to winter hosts where they give birth to oviparous females. Many of the migrants which develop on *Chenopodium album* do not change host species, but may migrate to another plant of the same kind. They take up a position on the under side of the leaf and begin feeding. Here the young oviparæ are born and developed to maturity. At the same time the apterous viviparous females on *Chenopodium album*, feeding along the smaller stems and flower corymbs, are giving birth to young which develop into winged males. On the under surface of leaves of *Rumex* and *Arctium* apterous viviparæ, alatae, males and oviparous females may be taken at one and the same time. It is from these herbaceous plants that some of the males migrate, in late October and November, to *Viburnum opulus*, *Euonymus atropurpureus*, *Hydrangea*, etc., and mate with the mature oviparæ on these plants. Egg deposition takes place in late October and November. It will be noticed that *Chenopodium album* appears in the table for each month but May. In April, it is only as dried stems, upon which eggs are found, that the plant is listed. The aphids have not been taken feeding on this host until June. In October, *Capsella*, *Galinsoga*, and *Stellaria* serve as hosts in certain locations near heavily infested *Chenopodium* plants. With the killing of *Chenopodium album* by frost in late October and November, the apterous viviparæ and young males migrate to these plants and complete their development. At other times during the summer these plants have not been recorded as hosts nor have I found oviparæ or eggs upon them.

In European countries, the spindle-tree *Euonymus europæus* is the favored host but with the absence of any numbers of that shrub in some sections of America, *Aphis rumicis* has evidently adapted

itself to our conditions and hence the choice as here described, of such a winter host as *Chenopodium album*. Another difference which this insect encountered in its food plants was the absence of the poppy (*Papaver* sp.) in the wild state in Eastern and Central United States.

NATURAL ENEMIES

Aphis rumicis does not increase without check throughout the season because certain parasitic and predaceous enemies reduce the numbers, in some instances destroying an entire colony on a plant. The parasites are particularly common in July and August. I reared *Asaphes americana* Gir. (det. Gahan) from parasitized aphids in August. This species has been recorded as a parasite of *Aphis rumicis* by Girault (39). *Lysiphlebus testaceipes* Cress. (det. Gahan) was bred quite frequently from *Aphis rumicis*. Although this parasite apparently has not been coupled with *rumicis* in literature, Mr. Gahan states that he has frequently determined it from this host. I reared two species of *Hymenoptera* which are probably secondary parasites: *Pachyneuron siphonophoræ* Ashm. (det. Gahan) perhaps a parasite of *Lysiphlebus*, and a Cynipid of which Mr. Weld says, "may be *Charips*, *Hemicrisis*, or *Phænoglyphis*." Specimens were also bred of *Aphidencyrthus* sp. (det. Gahan) Mr. Gahan says that no species of *Aphidencyrthus* has been recorded from *Aphis rumicis* and that it may or may not be a secondary parasite.

On June 7, 1923, many individuals of *Aphis rumicis*, with orange-colored mites clinging to them, were taken on *Arctium lappa*. Dr. Ewing wrote me about these as follows: "The mites belong to a species of *Bochartia* of the family Erythræidæ and are probably the young of one of our common species. Mites of the genus *Bochartia* parasitize aphids in their larval stage. In the nymphal and adult stages these mites are predaceous."

The predaceous beetles which were taken feeding on *Aphis rumicis* were *Megilla maculata* DeG., *Adalia bipunctata* Linn., *Hippodamia convergens* Guer., and *Coccinella 9-notata* Herbst. Larvæ of syrphid flies and lace-wing flies were taken devouring numbers of the aphids.

SUMMARY

Aphis rumicis Linn. has been known in literature under a large number of names because of its polyphagous habits and because of the early belief that species of aphids were largely confined to

single species of hosts. Nineteen of these names are listed here as synonyms. In Europe, the species has been known as a serious pest of varieties of beans, *Vicia faba*, Shirley poppies, mangolds, and *Euonymus*. In America, it seriously infests *Viburnum opulus* in the spring, *Euonymus*, nasturtiums, seed stalks of beets and spinach, and horse beans, where this crop has been introduced. It also lives on a large number of weeds.

During these studies, intermediates of viviparous females, oviparous females, and males have been found and described. The spring and fall migrants are morphologically distinct. Data from cage experiments correlated with field notes have demonstrated the presence of two distinct types of life cycles: one having woody shrubs as primary hosts upon which ova are deposited and the first generations develop in the spring with herbaceous plants as secondary hosts; the other having herbaceous plants such as *Chenopodium album* and *Rumex* as primary hosts and other herbaceous plants with the above named as secondary hosts. Five primary hosts have been added to the list upon which this insect has been known to winter and these records serve to clarify the reasons for the prevalence of this insect in sections where the primary hosts, previously reported, are scarce. The evidence seems to indicate that physiological species are not present.

From the detailed life history experiments it is found that *Aphis rumicis* Linn. may have a maximum of 20 first-born generations in Pennsylvania and a minimum of 12 last-born generations. The model number of first-born generations for four seasons was 19. The average length of the larval periods was 2 days for the first instar, 2 days for the second instar, 2 days for the third instar, and 2 days for the fourth instar. The length of time which elapsed between the birth of viviparous females and the date of birth of the first young varied according to the time of year in which they appeared and is presented in graphical form. This period ranged from 7 days in July and August to 20 days in late October and early November, with a mean developmental period of 10.5 days for all seasons. The average length of the productive period was 12.6 days. The total number of young produced by one female ranged from 2 to 105 individuals with an average of 24.6 young per mother. The maximum number of young borne by one mother in a single day was 13 and the average number born to one female in a day was 2.1 young. The total length of life for 76 females averaged 23.3 days.

Neither the records made on generation experiments nor notes taken in the field serve to clarify the problem as to what factor or combination of factors actually induces the appearance of winged forms although I feel that the appearance of the spring and fall migrants is more or less linked up in some way with temperature conditions. The copulation experiments between males taken from one host with females from a different host, while inconclusive in themselves, are of interest and value when correlated with the results of transfers of the viviparous females. Oviparae from woody shrubs, when transferred to herbaceous plants, continued to develop and deposit ova on the latter.

The following parasitic and predaceous enemies of *Aphis rumicis* were bred: *Asaphes americana* Gir., *Lysiphlebus testaceipes* Cress., *Pachyneuron siphonophoræ* Ashm., a Cynipid, *Aphidencyrthus* sp., *Bochartia* sp., *Megilla maculata* DeG., *Adalia bipunctata* Linn., *Hippodamia convergens* Guer., and *Coccinella 9-notata* Herbst.

BIBLIOGRAPHY

- (1) Amyot, C. J. B.
1847. Ann. Soc. Ent. Fr., 2 me. Series, V, 478.
- (2) Buckton, G. B.
1879. Monograph of British Aphides, II, 81.
- (3) Baker, A. C. & Turner, W. F.
1915. Proc. Ent. Soc. Wash., XVII, 42.
- (4) ————
1919. Journ. Agr. Res., XVIII, 6, 317.
- (5) Bethune, C. J.
1909. Ont. Dept. Agr. Bul. 171, 13.
- (6) ————
1917. Ont. Dept. Agr. Bul. 251, 11.
- (7) Bonnet, C.
1779. D'Hist. Nat., 1, 6.
- (8) Britton, W. E.
1916. Conn. Rpt. 15, 191.
- (9) ————
1917. Conn. Rpt. 16, 104.
- (10) ————
1923. Conn. Geol. & Nat. Hist. Survey, Bul. 34, 296 (Patch).
- (11) Cory, E. N.
1918. Penins. Hort. Soc. Trans., 31, 75.
- (12) Crosby, C. R. & Leonard, M. D.
1918. Man. Veg. Gard. Ins., 76.
- (13) Curtis, J.
1860. Farm Insects, 355.
- (14) Das, Bashambar
1918. Aphid. of Lahore, Mem. Indian Mus., VI, 203 (van der Goot).

- (15) Davidson, J.
1914. Ann. Appl. Biol. I, 118.
- (16) ———
1921. Ann. Appl. Biol., VIII, No. 1, 51.
- (17) ———
1921. Bul. Ent. Res., XII, pt. 1, 81.
- (18) ———
1921. Roy. Dub. Soc., Sci. Proc., n. ser. 16, Nos. 25-29, 304.
- (19) ———
1921. Ann. Appl. Biol., IX, No. 2, 135.
- (20) ———
1923. Ann. Appl. Biol., X, No. 1, 35.
- (21) Davidson, W. M.
1916. Journ. Ec. Ent., IX, 454.
- (22) Davis, J. J.
1911. Univ. of Neb. Studies, XI, No. 3, 18.
- (23) De Geer, Carl.
1773. L'Hist. des. Ins. III, 58.
- (24) De Ong, E. R.
1918. Univ. Calif. Agric. Exp. Sta. Bul. 294, 347.
- (25) Essig, E. O.
1915. Calif. Hort. Bul. IV, No. 4, Suppl., 94.
- (26) ———
1917. Univ. Calif. Publ. Ent., I, No. 7, 341.
- (27) Essig, E. O. & Kuwana, S. I.
1918. Proc. Calif. Acad. Sci., 4th ser., VIII, 73.
- (28) Fabricius, J. C.
1775. Syst. Ent., 735.
- (29) ———
1776. Gen. Ins., 303.
- (30) ———
1781. Spec. Ins., II, 390.
- (31) ———
1794. Ent. Syst., 213.
- (32) Fitch, Asa.
1870. Thirteenth Rpt. Nox. Ins. N. Y. for 1869, Trans. N. Y. Sta. Agr. Soc., XXIX, 495.
- (33) ———
Manuscript notes, Files Bur. Ent., U. S. D. A.
- (34) Fletcher, J.
1905. Can. Exp. Farms Bul. 52, 27.
- (35) Fonscolombe, B. de
1841. Ann. Soc. Ent. Fr., X, 162.
- (36) Gilbert, W. W. & Popenoe, C. H.
1919. U. S. D. A. Dept. Cir. 35, 7.
- (37) Gillette, C. P.
1910. Journ. Ec. Ent., III, 406.

- (38) Gillette, C. P. & Baker, C. F.
1895. Colo. Agr. Exp. Sta. Bul. 31, Tech. Ser. 1, 121.
- (39) Girault, A. A.
1916. Can. Ent., XLVIII, 342.
- (40) Hausmann, F.
1802. Illig. Mag., I, 439.
- (41) Haviland, Maud D.
1919. Proc. Chambr. Phil. Soc., XIX, pt. V. 226.
- (42) Hunter, W. D.
1901. Ia. Agr. Exp. Sta. Bul. 60, 104.
- (43) Headlee, T. J.
1919. N. J. Exp. Sta. Cir. 107, 7.
- (44) —————
1919. N. J. Hort. Soc. Proc., 44, 79.
- (45) Hayhurst, P.
1909. Ann. Ent. Soc. Am., II, 11, 97.
- (46) Kaltenbach, J. H.
1843. Mon. der Fam. der Pflanzenlause, 81.
- (47) Koch, C. L.
1857. Die Pflanz. Aphid., 50.
- (48) Kirby, W. and Spence, W.
1826. Introd. Ent., I, 175.
- (49) Linnæus, C.
1746. Faun. Suec., 217.
- (50) —————
1758. Syst. Nat. Ed. X, 451.
- (51) —————
1761. Faun. Suec. Ed. Alt. Auct., 259.
- (52) —————
1767. Syst. Nat. Ed. XII, I, 734.
- (53) Lefroy, H. M. and Howlett, F. M.
1909. Indian Ins. Life, 747.
- (54) Matsumura, S.
1918. Jour. Coll. Agr. Sapporo, VII, pt. 6, 357.
- (55) Mason, A. C.
1922. Fla. Ent., VI, No. 2, 25.
- (56) —————
1923. Fla. Ent., VII, No. 1, 1.
- (57) Mosley, O.
1841. Gard. Chron., I, 628, 747.
- (58) Mordwilko, A.
1899. Horæ Russ. Ent. Obsch., XXXI, 271.
- (59) —————
1907. Biol. Centralb., XXVII, 807.
- (60) Oestlund, O. W.
1887. Geol. and Nat. Hist. Surv. Minn., Bul. 4, 61.
- (61) —————
1922. 19th Rpt. Sta. Ent. Minn., 129.

- (62) Ohlendorf, W.
1917. Ms. Library Cornell Univ.
- (63) O'Kane, W. C.
1916. Injurious Insects, 201.
- (64) Orton, W. A. and Chittenden, F. H.
1917. U. S. Farm. Bul. 856, 29.
- (65) Osborn, H. and Serrine, F. A.
1893. Ia. Agr. Exp. Sta. Bul. 23, 901.
- (66) Patch, Edith M.
1912. Me. Agr. Exp. Sta. Bul. 202, 177.
- (67) _____
1913. Me. Agr. Exp. Sta. Bul. 220.
- (68) _____
1914. Me. Agr. Exp. Sta. Bul. 225.
- (69) _____
1917. Jour. Ec. Ent., X, 417.
- (70) _____
1918. Me. Agr. Exp. Sta. Bul. 270.
- (71) _____
1919. Me. Agr. Exp. Sta. Bul. 282.
- (72) Passerini, J.
1863. Aphididæ Italicæ, 37.
- (73) Riley, C. V. and Monell, J.
1879. Bul. U. S. Geol. Surv., V, No. 1.
- (74) Sanborn, C. E.
1904. Kan. Univ. Sci. Bul. III, 47.
- (75) Sanderson, E. D.
1908. U. S. Year Book, 570.
- (76) _____
1912. Insect Pests, 317.
- (77) Schrank, F.
1801. Faun. Boica, II, pt. 1, 111.
- (78) Schouteden, H.
1906. Mem. de la Soc. Ent. de Belg., XII, 226.
- (79) Scopoli, J. A.
1763. Ent. Carn., 136.
- (80) Siebke, H.
1874. Enum. Ins. Norveg., 46.
- (81) Smith, L. B.
1917. Va. Truck Sta. Bul. 23, 504.
- (82) Stephens, J. F.
1829. Syst. Cat. Brit. Ins. 365.
- (83) Stewart, George
1919. Utah Agr. Coll. Cir. 37, 38.
- (84) Swain, A. F.
1919. Univ. Calif. Publ. Ent., III, 1, 101.
- (85) Takahashi, R.
1921. Aphid. of Formosa, pt. I, 47.

- (86) Talbert, T. J.
1917. Mo. Ext. Cir. 15, 8.
- (87) Theobald, F. V.
1911. The Entomologist, XLIV, 19.
- (88) _____
1912. Jour. Bd. Agr., XIX, 466.
- (89) _____
1912. Jour. Econ. Biol., VII, 94.
- (90) _____
1914. Bul. Ent. Res., IV, 329.
- (91) _____
1916. Can. Ent., XLVIII, 234.
- (92) _____
1923. Bul. Soc. Roy. Ent. D'Egypte, 1922, 47.
- (93) Thomas, C.
1879. 8th Rpt. Ill. Sta. Ent., 88.
- (94) Uichanco, L. B.
1921. Psyche, XXVIII, 95.
- (95) Van der Goot, P.
1915. Kennt. Holland Blattl., 220.
- (96) Wadley, F. M.
1923. Ann. Ent. Soc. Am., XVI, 4, 279.
- (97) Walker, F.
1850. Ann. and Mag. of Nat. Hist., V, Ser. 2, 17.
- (98) _____
1852. Cat. Homop. Brit. Mus., IV, 981.
- (99) Wilson, H. F. and Vickery, R. A.
1918. Trans. Wis. Acad. Sci., XIX, 150.

PLATE I

Fig. A. Line of first-born generations, *Aphis rumicis*, Bustleton Pa., 1923.

Fig. B. Relation between the mean temperature and the developmental period of viviparous females of succeeding generations.

PLATE I

Gen. No.	Length Days	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
1	14x	16-18-?								
2	12x	16-28-...								
3	17x	27	14							
4	28	10	7							
5	30		25	24						
6	35		3	8						
7	16		11	27						
8	22			20	12					
9	16			29	14					
10	16				7	25				
11	16				14	30				
12	14				22	4				
13	12				30	11				
14	13				10	23				
15	23				22	14				
16	31					31	1			
17	22					10	2			
18	60						22	20		
19	33						5	7		
20	30x							21	24-?	A

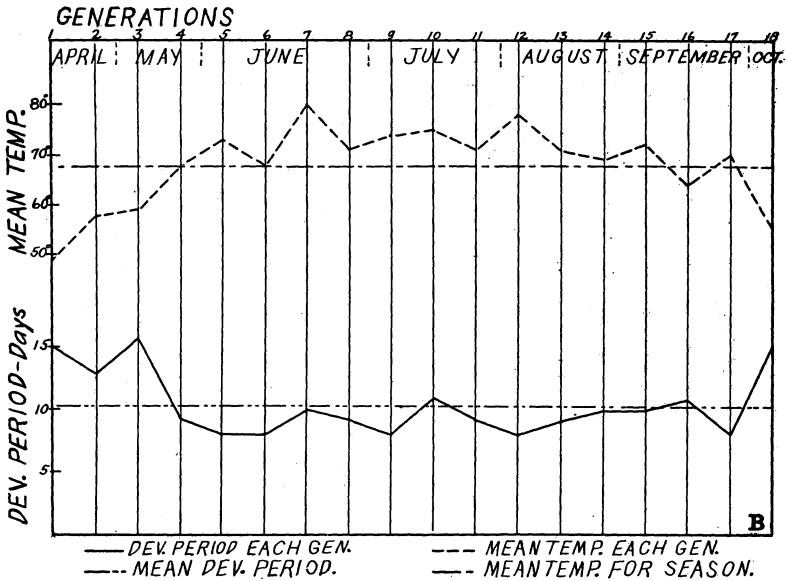


PLATE II

- Fig. A. Winged Male, *Aphis rumicis*, greatly enlarged; B, Antenna of same; C, Cornicle; D, Cauda; E, Hind Tarsus.
- Fig. F. Winged Viviparous Female, *Aphis rumicis*, greatly enlarged; H, Cornicle; I, Cauda; J, Hind Tarsus.

PLATE II

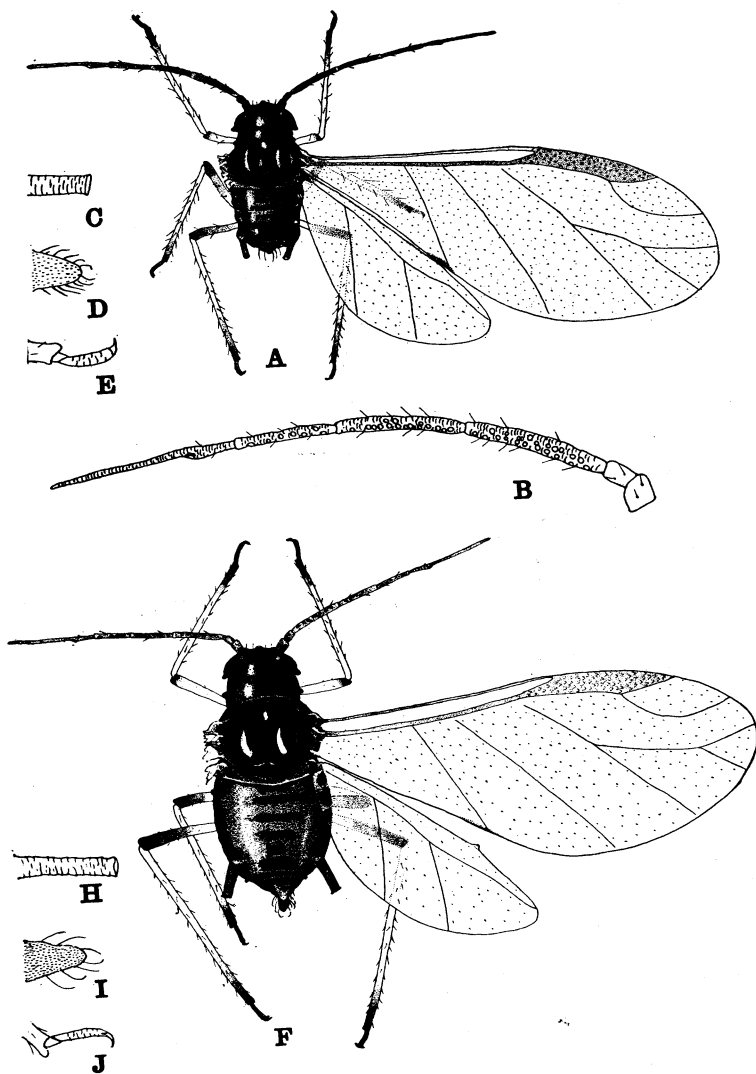
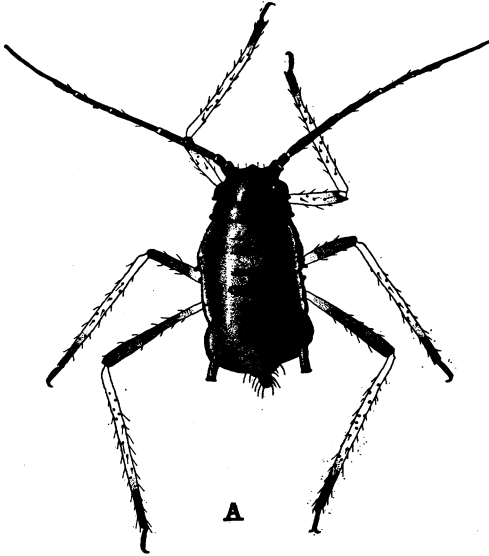


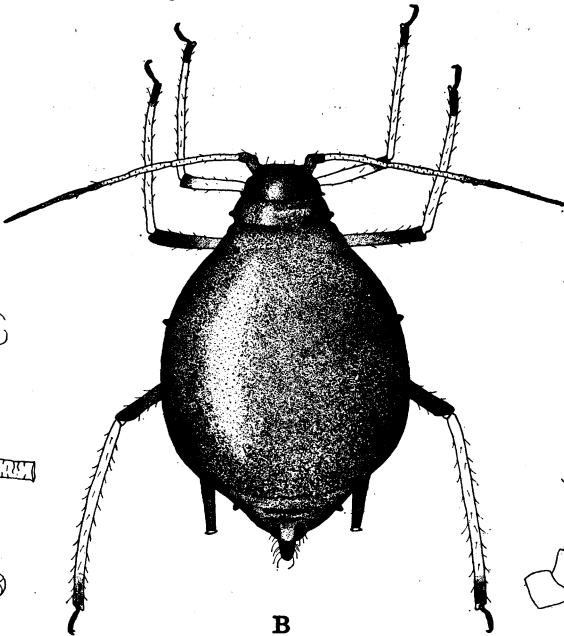
PLATE III

- Fig. A. Intermediate Male, *Aphis rumicis*, greatly enlarged. Only traces of winged characters present are tiny buds and a slight sign of division into thoracic lobes.
- Fig. B. Apterous Viviparous Female, *Aphis rumicis*, greatly enlarged; C, Antenna of same; D, Cauda; E, Cornicle; F, Hind Tarsus.

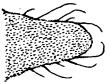
PLATE III



A



B



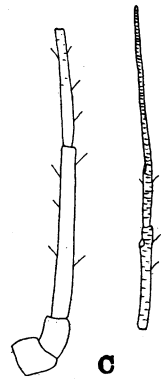
D



E



F



C



PLATE IV

Figs. A, B, C. Antennal segment III of winged males from *Chenopodium album* showing variation in number and arrangement of sensoria.

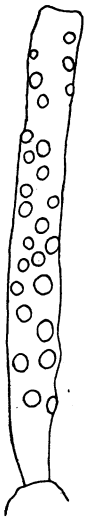
Fig. D. Antennal segment III of spring migrant from *Rumex crispus*.

Fig. E. Antennal segment III of fall migrant from *Rumex crispus*.

Fig. F. Pupa, *Aphis rumicis*, greatly enlarged. Note the white pulverulent patches on the abdomen.

Fig. G. First Instar Larva, *Aphis rumicis*, greatly enlarged.

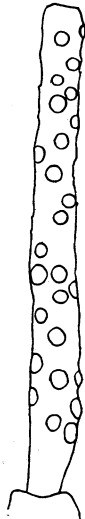
PLATE IV



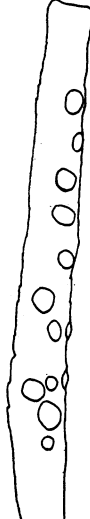
A



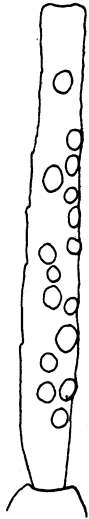
B



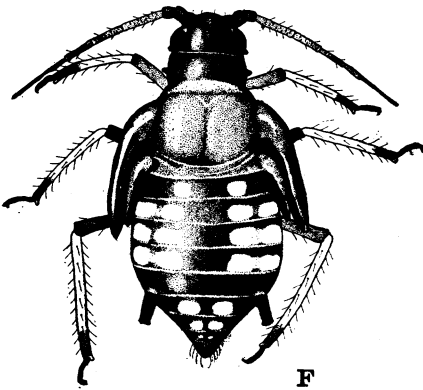
C



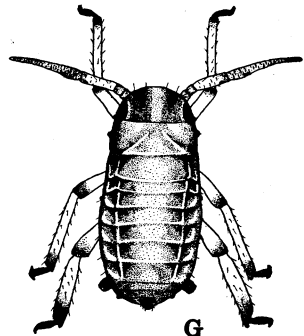
D



E



F



G

PLATE V

- Fig. A. Intermediate Male, *Aphis rumicis*. Wings represented by conspicuous pads.
- Fig. B. Oviparous Female, *Aphis rumicis*. Note swollen hind tibiae. C, Cornicle of same; D, Cauda; E, Hind Tarsus; F, Antenna.
- Fig. G. Intermediate. A viviparous female with characters of winged form represented in thoracic characters, wing pads, and markings on abdomen.
- Fig. H. Intermediate. Oviparous female with eggs present in abdomen. The specimen has the slender hind tibiae characteristic of the viviparous female.
- Fig. I. Stem Mother, *Aphis rumicis*; J, Cornicle of same; K, Cauda; L, Hind Tarsus; M, Antenna.

PLATE V

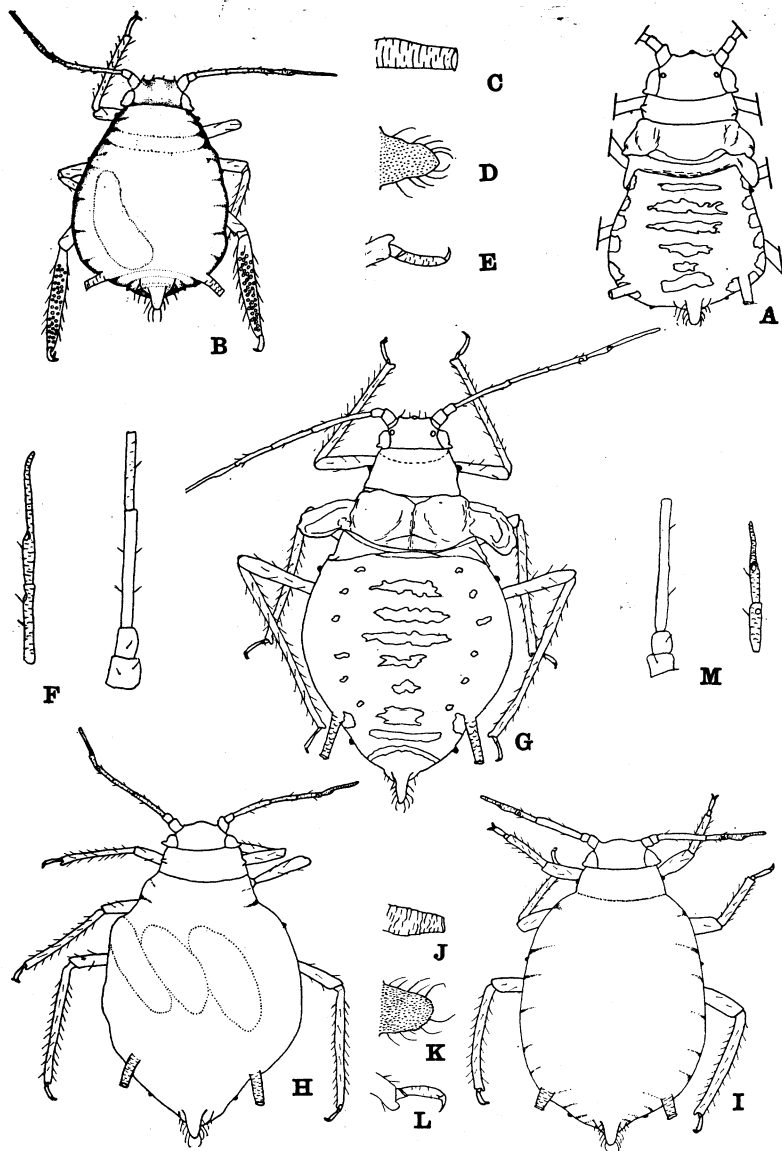


PLATE VI

Leaves of *Tropæolum minus* infested with colony of *Aphis rumicis*. Note the pupæ with white pulverulent spots on abdomen.

PLATE VI



PLATE VII

Plants of *Arctium lappa* infested with colony of *Aphis rumicis*.

PLATE VII



PLATE VIII

- Fig. A. Eggs of *Aphis rumicis* on stem of *Chenopodium album*. The stem was broken and healed during the growing period.
- Fig. B. Colony of *Aphis rumicis* on stem of *Chenopodium album*.
- Fig. C. Colony of *Aphis rumicis* on the flower-stems of *Dahlia* attended by ants.

PLATE VIII

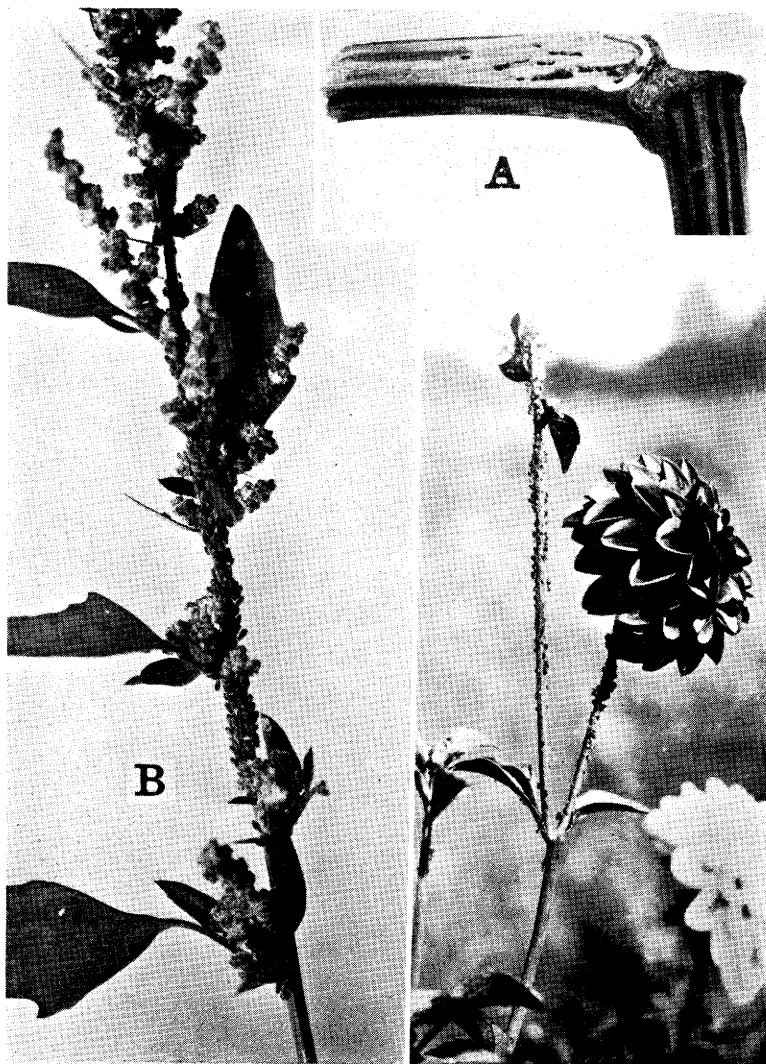
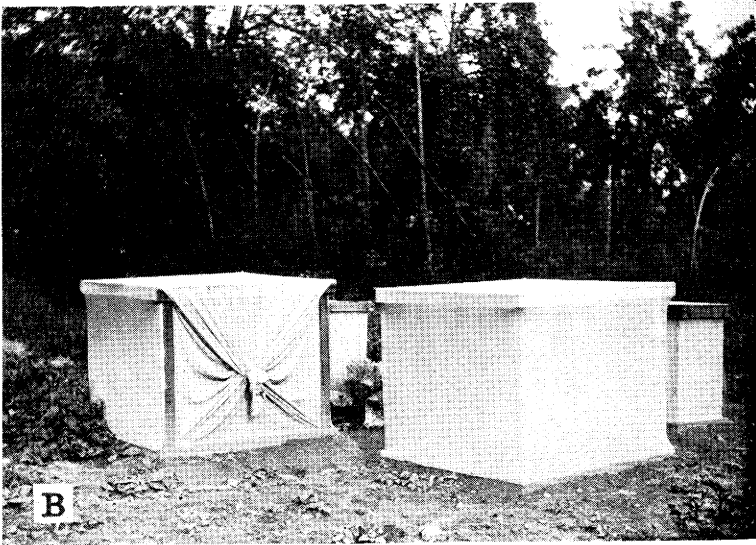
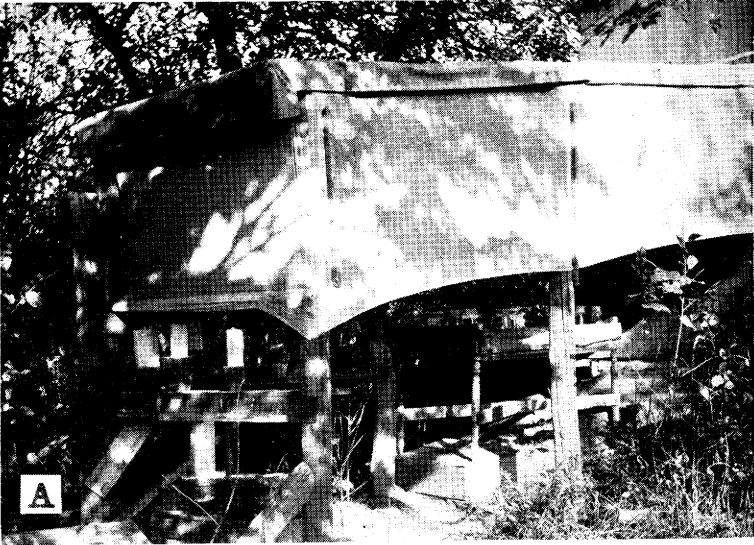


PLATE IX

Fig. A. Type of insect cages used in the field for rearing *Aphis rumicis*.

Fig. B. Insectary used for life history experiments.

PLATE IX



UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor



VOLUME XI

NUMBER 3

THE DEVELOPMENT OF THE RENAL PORTAL SYSTEM IN *CHRYSEMYS* *MARGINATA BELLII* (GRAY)

by

WILLIS DE RYKE, Ph.D.

PUBLISHED BY THE UNIVERSITY, IOWA CITY



Dona Miss. Lib.
7-31-1925

THE DEVELOPMENT OF THE RENAL PORTAL SYSTEM IN *CHRYSEMYS MARGINATA* BELLI (GRAY)

I. INTRODUCTION

1. PURPOSE AND SCOPE

During the progress of evolution among the vertebrates, for some unknown reason the renal portal system has been discarded. We find it present in a typical form in fishes, Amphibia, snakes, lizards and possibly some Chelonia. In birds it is considerably modified, if present at all, and is apparently entirely absent in mammals. Whatever may have been the advantage or disadvantage of the renal portal system, the change has been made and doubtless the transition lies somewhere in the Reptilia, probably the Chelonia. Its presence in a typical form in turtles has been doubted although many eminent workers in the fields of comparative anatomy and embryology have strongly suspected that the adult Chelonia, or at least some species of them, possess a true renal portal system.

The study of the veins associated with the kidneys of the turtle *Chrysemys marginata belli* (Gray) and their development was undertaken to ascertain the presence or absence of a renal portal system in the adult of this species, to trace its development if present and the development of certain veins closely related to the kidneys and which would probably be involved in the embryological formation of such a system. It was also desirable to compare to some extent the development in this form with that of certain other related forms.

The solution to the problem of presence or absence of the renal portal system in the adult lay in the study of the adult system of veins related to the kidney and a determination of the presence or absence of a capillary network within the adult kidney which permits the passage of blood on its way from the body capillaries to the heart.

The embryological study involved the development of the vertebral veins, posterior cardinals, renal advehens anterior, renal advehens posterior, subcardinals, extreme posterior region of the post-cava and the venous network of the kidney.

I wish here to acknowledge my indebtedness and express my thanks to Dr. Frank A. Stromsten for his constant assistance, advice, and criticism and to Prof. Gilbert L. Houser for his many helpful suggestions and provision of adequate laboratory facilities to carry on this work.

2. HISTORICAL

A comparatively small amount of work has been done in tracing the detailed development of the venous system of the turtle. It is especially striking that such an important and interesting question as the presence or absence of a renal portal system and its development as found in *Chelonia* should have remained uninvestigated. The most noteworthy attempts by the early workers to trace the development of the venous system of *Chelonia* were those by Agassiz, ('57) and Rathke, ('48). Perhaps the reason for these early workers not having investigated this system is due to the scarcity of material or what is more probable, the lack of the modern methods of technique.

A much greater amount of work has been done on the development of the venous systems of Selachians, Amphibians, snakes and lizards. For these extensive contributions we are indebted to Goette, Hochstetter, Hoffmann and Rathke. The condition as found in cyclostomes has been described by Rathke, Retzius and Johannes Müller. The presence of a renal portal system in fishes was first discovered by Jacobsen, one of the pioneer investigators. He found various expressions of the renal portal system which he could classify into three forms as follows: (1) The veins of the skin and body region discharge into the kidney while the caudal vein does not branch into the kidney but discharges into the right cardinal vein. (2) Similar to the first except that the caudal vein branches in the kidney. (3) A modification of the former two in that the caudal vein or another vein unites with the portal vein of the liver. Hyrtl recorded the condition as found in bony fishes and especially that of *Lepidosiren paradoxa*.

The principal work on the development of the veins in Selachians has been done by Balfour, Hochstetter and Hoffmann. Hoffmann in his work "Zur Entwicklungsgeschichte des Venensystems bei den Selachiern" gives an account of the development of the venæ omphalo-mesentericæ, vena subintestinalis and venæ cardinales. He finds that the beginnings of the posterior cardinal veins are closely bound to the anlage of the mesonephros and in early stages

are comparatively free from anastomoses with each other but later freely anastomose. In an embryo of 20 mm. the posterior cardinals have already formed and begun to anastomose with the vena subintestinalis caudalis producing a renal portal system. Balfour records the vena subintestinalis as appearing ventral to the alimentary tract, being the first large venous trunk to form in Selachian embryos and terminating shortly before the end of the tail. It bifurcates at the cloaca, uniting again anteriorly. The anterior part then atrophies, the posterior part remaining and becoming the caudal vein. As soon as the cardinal veins appear the caudal vein unites with them. This is accomplished by the degeneration of the anterior portion of the anal ring and the union of the two posterior portions with the posterior cardinal veins on either side. The anastomosing branches between the caudal vein and the posterior cardinal veins pass through the mesonephros and eventually break up into a capillary network and a renal portal system is established. According to Hochstetter the development of the renal portal system in Selachians is as described by Balfour.

The development of the renal portal system in an Amphibian has been traced by Goette in *Bombinator igneus*. According to his description the posterior cardinal veins which open anteriorly into the duct of Cuvier unite posteriorly with the caudal vein. At this union the iliac veins join the system. In the meantime the mesonephros has developed in the region of the union. The cardinal veins fuse close to the mesonephros and the posterior portion forms a part of the postcava. The anterior part of the postcava develops independently. This is followed by the atrophy of the anterior region of the mesonephros and the posterior cardinals. The veins which first opened into the posterior cardinals now lose their connections and form the renal advehentes. The iliac veins become connected with a newly developed vein, the abdominal, and in this manner have connection with the postcava through Jacobsen's vein and with the anterior abdominal vein through the epigastric vein. In this manner a renal portal system is laid down.

Probably the most valuable work touching on the renal portal system of reptiles has been done by Bojanus, Jourdain, Nicolai, Hochstetter, Hoffmann, Rathke and Stromsten.

Jourdain ('59) in describing the renal portal system of the kidney of an adult Ophidian details its arrangement as follows. After picking up the important vessels, mesenteric vein and cloacal

veins as well as a vein from the tail, the renal portal vein proceeds, accompanied medially by the ureter and laterad by the vas deferens or oviduct, in a circuitous manner over the kidney. In its course it picks up small veins from the ureter and vas deferens (oviduct), a vein parietalis anterior and a varying number of intercostal-spinalis veins. Each of these veins runs along the edge of the kidney accompanied by the ureter which is on the inside. Their branches are numerous and disappear for the most part in the notches between the small lobes branching out like dendrites between the canals of the kidney. The advehent veins of the kidney branch and become smaller and smaller until they finally lose themselves in the forward part of the kidney. From the anastomosis of the efferent veins, a system, the renal revehent arises which courses anteriorly from the kidney along with the one from the opposite side and unites with the postcava.

Rathke contributed to our knowledge of the venous system of *Tropidonotus natrix* ('39), the crocodile ('66) and the turtle ('48). His account of the development of the venous system of the natter contains a very good description of the posterior venous system development, a resumé of which follows. In the development of the natter the caudal vein is divided early and each branch unites with the posterior cardinal. The postcava is developed as a branch of the common stem of the right omphalo-mesenteric vein and the right vertebral vein lying in the caval mesentery and proceeding along the dorsal wall on the median side of the mesonephros. The mesonephroi then begin to separate from the body wall and degenerate from anterior to posterior. This results in the formation of the vertebral veins which are formed from the anastomoses between the segmental veins on both sides of the vertebral columns. These vertebral veins later atrophy in the posterior region and practically disappear leaving little or no trace. With the separation of the mesonephroi from the dorsal body wall they begin to degenerate, and the cardinal veins to atrophy anteriorly losing their connection with the jugulars.

The caudal vein with its two branches and the posterior cardinals with their tributaries comprise the advehent system. The vena cava and its two large branches comprise the revehent system.

Hochstetter ('93) studied the development of several species of lizards giving a splendid account of the development of *Lacerta agilis* and *Lacerta viridis*. According to his observations on the

development of *Lacerta agilis*, in a stage where the intestine is closed to a point where the liver is well developed, the posterior cardinals are already well developed, being clearly marked in the posterior region of the mesonephros but broken up into blood sinuses which lie between the mesonephric tubules in the anterior region. At some points the posterior cardinals appear to be ventral, at others lateral and in the posterior region clearly dorsal to the mesonephroi. These veins also receive blood from the segmental veins. With the increase in compactness of the mesonephroi the veins change their relations.

With the growth of the tail region the caudal vein becomes of importance. It enlarges and bifurcates dorsally and anteriorly to the blind end of the intestine, the two branches running along the median sides of the mesonephroi. These two veins anastomose with each other anterior to the omphalo-mesenteric artery and connect freely with the venous network of the mesonephroi.

With the formation of the postcava by the union of the omphalo-mesenteric veins with the unpaired portion of these veins the branches of the caudal vein lose their connections and unite with the posterior cardinals. A degeneration of the anterior end of the mesonephroi and the atrophy of the anterior portion of the posterior cardinals now make the rest of the posterior cardinals and the caudal vein and its branches the afferent veins of the mesonephroi.

The mesonephroi now begin to separate anteriorly from the dorsal body wall. This process continues posteriorly. The postcava bifurcates and runs between the mesonephric bodies receiving several branches. The postcava and its branches then comprise the revehent system of the mesonephroi.

While this is taking place the venous network of the anterior end of the mesonephros becomes disconnected from the duct of Cuvier and becomes connected to a row of segmental, anastomosing veins which have gradually developed as a result of the separation of the mesonephroi from the dorsal body wall. The chains of anastomosing vessels become larger as the mesonephroi degenerate and lie on either side of the vertebral column ventral to the rib anlagen. With the degeneration of the anterior portion of the mesonephroi the number of connecting veins decreases until only a few of them at the posterior end of the mesonephroi remain. The chains of veins form longitudinal anastomoses and also anastomose with each other.

The embryological development in the other forms, including *Lacerta viridis* on which Jourdain had worked, was found in general to parallel that of *Lacerta agilis*, the difference being in minute details of development.

The latest work of consequence on the development of the posterior portion of the venous system of a reptile is that of Stromsten ('05). He traced the development of the veins in the posterior region of the turtle *Kinosternon pennsylvanicum*. His studies included the development of the hepatic portal system and to a considerable extent the development of the umbilicals, abdominals and the larger veins involved in the development of the renal portal system.

According to Stromsten, the posterior cardinals and subcardinals are already formed in the youngest embryo studied, an embryo of 7.4 mm. crown rump measurement. The posterior cardinals extend from the caudal termination of the mesonephric ducts along the entire length of the mesonephroi. At the caudal termination of the mesonephric ducts the posterior cardinals receive a number of small branches from the tail region, the last dorsal intersegmental branch and a stout anastomosing branch from the subcardinal of the same side. The portion of the posterior cardinals between the cranial end of the mesonephros and the sinus venosus is broken up into two or three vessels.

In a 7.4 mm. embryo the subcardinals are formed and connect with the posterior cardinals by numerous anastomoses but do not connect with each other. With growth the two branches of the caudal vein unite with the subcardinal veins, establishing a renal portal system. With continued development, the forking caudal vein loses its connection with the subcardinals and unites with the posterior cardinals. The postcava develops and the course of the blood is reversed in the portal system of the mesonephroi.

The posterior vertebral veins are fused dorso-segmental branches of the posterior cardinals and lie dorsal to the rib anlage.

The anterior and posterior renal advehent veins of the kidneys represent the remains of the posterior cardinals.

3. MATERIAL AND METHODS

Adults

Ample material for the study of this problem was found in the region of Lake Okoboji located in the northwestern part of the State of Iowa. I was quite fortunate to find that a laying ground

for *Chrysemys marginata belli* (Gray) was conveniently adjacent to the grounds of the Lakeside Laboratory on Miller's Bay. The turtles swarmed up the sloping gravel bank usually between the hours of four to eight of an evening to lay their eggs, making a splendid opportunity for observations, recording the time of laying and marking the nests.

Before proceeding with the study of the embryonic changes involved in the developing venous system the adult venous systems of about twenty-five turtles were studied, special attention being given to the veins related to the kidneys. That the blood vessels might be in as expanded condition as possible and better injections assured the animals were killed with a concentrated solution of chloral hydrate.

The injection media used most successfully were a yellow starch paste mass and a colored gelatin mass. The yellow starch mass was prepared according to Guyer.¹ A carmine gelatin injection mass was prepared according to Walker's variation as given by Guyer,² and also a blue gelatin injection mass as given by Guyer.³ The setting of the gelatin during the process of injection was prevented by adding a small amount of potassium iodide. The injection masses were forced into the vessels by means of a metal syringe or by the gravity method, both of which were quite adequate. Immediately after injection the specimens were plunged into a ten per cent formalin solution, thus coagulating the gelatin.

The necessity for determining the arrangement of the veins within the kidney is quite obvious. The small size of the veins entering or leaving the kidney makes it impossible to remove the kidney and inject. For this reason it was necessary to inject a large portion of the venous system at sufficiently high pressure to guarantee the filling of the vessels of the kidney.

Injections of yellow starch paste were made and dissection carried out as far as possible under the binocular microscope. This method however had its limits in that the relations of the smaller and more numerous vessels were lost through the necessary destruction of some of them during dissection.

In order to preserve these smaller vessels a less mechanical method was sought. The first attempts were by means of an injection of

¹Guyer—Animal Micrology, p. 92.

²Guyer—Animal Micrology, p. 83.

³Guyer—Animal Micrology, p. 84.

ozokerite wax. The greatest difficulty encountered here was that a temperature sufficiently high to keep the wax in a liquid condition had to be maintained. The metal syringe, the wax, and the specimen had to be at this temperature to prevent the hardening before complete injection. This difficulty was overcome by placing the specimen and apparatus in water at the temperature of the melting point of the wax. With rapid operation the injection could be made but by no means was success achieved at all trials.

These injected specimens were then cooled and the kidneys with their projecting blood vessels removed from the turtle. Some of them were then placed in artificial gastric juice and kept in an incubator until the digestion of the tissue was complete. Another method used for eliminating the tissue was that of corrosion to be discussed presently. Wax casts resulted which were very good for study but the difficulty of their preservation and their delicacy made it desirable to have a method whereby permanency might be gained.

In seeking a permanent injection mass celloidin was tried and found to be a fairly successful method but somewhat expensive as many failures of injection were unavoidable.

The method finally adopted and the most successful one was that of injecting a colored liquid celluloid. This injection fluid is prepared as follows. Sheet celluloid secured from discarded automobile curtains is thoroughly washed and cut into small pieces. About twenty grams of this is dissolved in 100 cc. of acetone and allowed to stand for twenty-four hours. Fifteen grams of camphor is then dissolved in this solution. This is then used as a stock solution and must be kept air tight. Before using this liquid as an injection medium it is thinned by the addition of acetone carrying a coloring agent. The size of the vessels to be injected determines the viscosity of the injection medium to be employed. The liquid was thinned to almost a watery viscosity when it was desired to inject capillaries. A large number of coloring agents were tried, the most satisfactory of which were found to be crystal violet, brilliant green and alkanet, all soluble in acetone.

This injection fluid on coming in contact with water forms a hard cast and does not readily break. With an increase in the percentage of camphor it may be made to take on the nature of rubber. This medium then produced the desirable characteristics since it is not brittle and stands considerable rough handling.

The turtles were killed by chloral hydrate and the plastron carefully removed. Injection was then made through the left abdominal vein after tying off the right, through the postcava, or through the left aortic arch after tying off the right. Not only single injections were carried out but double and triple injections of the colors were resorted to in all possible combinations.

After injection the specimens were immediately placed in cold water where they remained for twelve hours. This permitted the casts to become hard. The kidneys were then carefully removed with their protruding injected vessels and placed in artificial gastric or pancreatic juice in a suitable warming oven, or more commonly and with equal success they were subjected to the action of concentrated muriatic acid for twelve to eighteen hours. It was then possible to wash out in water the corroded tissue. This was accomplished by admitting a gentle flow down a stirring rod from an open tap or by carefully using a pipette, both of which methods proved satisfactory. For the extremely fine structure this method was slightly altered. After a large portion of the kidney substance had been corroded and washed out the kidneys were permitted to remain in the water for days until disintegration had taken place and the tissue practically removed itself from the meshwork of minute blood vessels. This method produced very beautiful casts, accurate to the minutest detail and of such a permanent nature that they could be studied without damage to them.

In addition to the study of the casts, the finer vascular structure of the kidney was studied by means of serial sections. These serial sections were made of the kidneys of fifteen specimens which had been injected under high pressure with a carmine gelatin mass or an aqueous solution of Berlin blue. Also a specimen just hatched was serially sectioned in the region of the kidneys, stained in borax carmine and mounted for study.

Embryos

Two entire summers were given over chiefly to securing material for the embryological study. No difficulty was encountered in locating the nests or securing eggs. The laying season was found to extend from the middle of June to about the twenty-fifth of July. The laying usually takes place between the hours of four to eight in the afternoon, the number of eggs in a clutch varying from five to fifteen and averaging about eleven.

During the summer of 1923 ninety-six nests of the painted turtle

Chrysemys marginata belli were located and during the summer of 1924 about fifty nests of the same species were located. From these eggs I was able to secure about twelve hundred embryos.

The desire for embryos of as many gradations in size as possible led to two plans for securing them. The first was to stake and record the nest at the time of laying and remove the entire clutch when embryos of this particular age were desired. The second was to stake nests through fifteen successive days of laying and remove two or three eggs from each nest every fifteen days. However no exact method for securing a graded series is possible owing to the fact that different conditions such as kind of soil, depth eggs were laid, amount of sunshine and shade alter the incubation period. Not only is this true of each nest but it is true of each egg in the nest, so it is possible to find a single clutch having embryos at various stages of development. Three pairs of twins were found during this period and it was quite interesting to find in each case that one of the twins had outgrown the other and in one case the larger was at least twelve times the size of the smaller.

The small embryos adhere closely to the shell making their removal somewhat difficult. It was found much more expedient to locate the minute embryo with a hand lens and cut around it through the shell, placing the entire piece, shell and embryo, in the fixing fluid. The embryo could then be easily separated from the shell after reaching the alcohols. The larger embryos could of course be easily removed from the shell and fixed.

Fixation was made in Bouin's picro-formol fluid or in chrom-aceto-formalin mixture. The length of time of fixation ranged from one hour to four hours, depending upon the size of the embryos. Just before using, two volumes of this mixture are added to one volume of formalin.

BOUIN'S PICO-FORMOL

Picric acid, saturated aqueous solution.....	75 parts
Formalin	25 parts
Acetic acid (glacial)	5 parts

CHROM-ACETO-FORMALIN MIXTURE

Chromic acid, 1 per cent solution.....	16 parts
Glacial acetic acid	1 part

These two fixing fluids were found to have a double advantage. They were excellent in fixing the tissues and in addition, the glacial acetic acid attacked and destroyed the greater part of the eggshell.

The embryos were then passed through the graded alcohols until seventy per cent was reached where they remained until they could be stained and sectioned.

The process of staining and sectioning was done at the State University of Iowa. A series of embryos was selected for sectioning. Each embryo was drawn by the camera lucida and the magnification recorded in order that reference might be obtained and measurements made. Some of the embryos were then stained *in toto* with borax carmine, passed through the graded alcohols, cleared in xylol, embedded in paraffin, sectioned and mounted. The majority of the embryos were passed through the graded alcohols, cleared in xylol, embedded in paraffin, sectioned, mounted, stained in Delafield's hemotoxylin and counterstained with Grubler's Orange G. acidulated slightly with acetic acid. In sectioning the embryos those from 1.2 mm. crown rump measurement to 16 mm. crown rump measurement were cut 20 microns. Those from 8 mm. to 12 mm. carapace length measurement were cut 20 microns. Those from 12 mm. to 14 mm. carapace length measurement were cut 25 microns and one with a 22 mm. carapace was cut 50 microns.

That the study of the sections might be supplemented by the study of injected embryos approximately one hundred embryos ranging in size from the earliest stages of development to the adult were injected with various fluids. The greatest difficulty encountered in this technique was to find an injection fluid whose viscosity was low enough to permit the complete injection of the finer vessels of the embryo and still not leave the vessels and penetrate the tissues. Certainly the most logical form of an injection fluid for this purpose would be some colloid solution or perhaps a celluloid injection. The latter was tried numerous times and in many degrees of concentration, but the fluid invariably hardened before complete injection of the finer capillaries. Considerable time was spent in search of a suitable colloid solution. Among the large number tried it was found the best results could be obtained by using Higgin's Black India Ink, an aqueous solution of Berlin blue or alkanet.

After several mechanical devices for injection of the embryos had been tried, it was found that the simplest type was the most successful. This consisted of a small rubber tube with a mouth-piece inserted at one end and a glass canula at the other. In the construction of this apparatus there is but one difficult feature; the

construction of the canula. This is done by drawing out a small glass tube into a hairlike capillary three or four inches long. By placing this under a microscope the point at which the space ceases and the solid glass begins may be determined. With a pair of scissors the tube may be cut at this point leaving a very fine hairlike capillary tube.

In using this mechanism the canula is carefully inserted in the rubber tube and the end dipped into the injecting fluid. The operator then with the mouthpiece in his mouth draws the fluid into the canula. Then while looking through a binocular the canula may be inserted in the heart, the sinus marginalis, the jugular vein, the umbilical vessels or any other clearly discernible vessel. The operator then applies pressure to the fluid, forcing it into the vascular system of the embryo. The canula after once being used must be kept in water to prevent the closure of the tube.

From the injected embryos three series were selected duplicating as nearly as possible the series which had been sectioned. The members of the first series were serially cross sectioned and mounted. Those of the second series were cut into thick longitudinal sections and mounted. The smaller members of the third series were used in whole mounts. By this means it was then possible to obtain a check on the study of the stained cross sections.

II. ADULT RENAL PORTAL SYSTEM

The right and left abdominal veins issue from the liver substance and lie on either side of the ventral median line. They run ventrally for a short distance but soon make a sharp turn in a posterior direction, lie immediately ventral to the peritoneum and course toward the ventral median line. They receive as tributaries during this part of their course, a small gastric vein, a vein from the pectoral muscles and a small vein from the tensor-pleuro-peritoneal muscle. They gradually approach each other in their course diverging again at a point just anterior to the pubis. Slightly posterior and ventral to this they are placed in communication by a transverse vessel lying ventral to the pubis and receiving branches from the obturator externus and pubo-plastinalis. Continuing posteriorly and diverging they angle in a dorsal direction following the curve produced by the pelvic girdle and carapace until they join the external iliac vein of their respective sides. In the latter part of their course they receive tributaries from the obturator

internus muscle, a large branch which anastomoses with the margino-costal vein of the carapace, a vein from the pubo-plastinalis muscle, a branch from the vastus femoras rectus muscle and the femoral vein. The abdominals unite with the circumflex iliac veins of their respective sides to form the external iliac veins.

The ischiadic vein leaves the thigh, passes into the pelvis and unites with the common coccygeal vein to form the circumflex iliac vein.

The circumflex iliac vein courses dorsally, receives the epigastric vein and unites with the abdominal vein of its side to form the external iliac vein.

The external iliac vein makes a sharp turn and courses toward the median line. Reaching the external border of the kidney it passes to the ventral surface where it unites with the renal advehentes.

The posterior renal advehent vein is formed by the union of a number of small branches bringing blood from the muscles of the pelvis, the caudal region and cloaca with its closely related organs. This vein then passes dorsally and anteriorly within the pelvis. Leaving the pelvis and reaching the posterior edge of the kidney it passes over and in close contact with the ventral surface of the kidney where it gives off afferent branches to the kidney and eventually anastomoses with the anterior renal advehent vein at a point where these two unite with the external iliac vein.

The anterior renal advehent vein, as a branch of the vertebral vein arises between the fifth and sixth ribs, receives the fifth intercostal vein and immediately passes to the ventro-lateral surface of the anterior portion of the kidney. As it courses along the surface of the kidney it gives off afferent branches and unites posteriorly with the renal advehent vein at a point where both are joined by the iliac vein.

For convenience of discussion the portions of the anterior and posterior renal advehent veins lying adjacent to the surface of the kidneys will hereafter be spoken of as the renal portal vein.

The vertebral veins arise as a bifurcation of a single vein in the region of the first thoracic vertebra and run posteriorly on either side of the spinal column. In their course they lie dorsal to the ribs and receive the first four intercostal veins and veins from the spinal cord. Between the fifth and sixth ribs the vertebral vein gives off a large branch, the anterior renal advehent vein. Pos-

terior to this branch they diminish considerably in size, give off numerous small branches to the kidneys and continue posteriorly gradually becoming smaller in diameter and eventually ending by receiving a number of minute branches from the extreme caudal region.

The postcava is formed between the kidneys by the union of two short thick veins. These in turn result from an anastomosis of veins leaving the kidney, the latter veins usually numbering three from the left kidney and two from the right, but frequently the reverse is true. The veins returning blood from the ovaries or testes unite with these veins in the region of their entrance into the kidney substance. The postcava leads anteriorly coursing away from the median line toward the duodenal flexure and enters the right dorsal lobe of the liver. Posterior to the kidneys there is no postcava.

The kidneys are a pair of lozenge shaped organs lying in the posterior dorsal curvature of the carapace, one on each side of the spinal column. They present three lobulated surfaces, a curved dorsal surface, a mesial surface and a latero-ventral surface. The surfaces are united with each other by rounded edges of considerable curvature.

The venous tributaries to the postcava arise from the mesial ventral edge of each kidney. These tributaries branch rapidly into smaller veins which enter the kidney substance and embed themselves between the lobules.

Closely adhering to the latero-ventral surface is the renal portal vein joined about midway by the external iliac vein which is partially buried between the kidney lobules. On the side in contact with the kidney the renal portal vein branches profusely, the afferent vessels entering the kidney substance between the lobules.

In an effort to determine the true nature of the connections between the renal portal vein and the postcava a heavy yellow starch paste mass under a constant pressure was injected into the postcava of a large number of specimens. In no case was I able to get the injection mass to pass through the veins of the kidney and appear in the renal portal vein. In another group of specimens the injection was carried out in the opposite direction by injecting into the left abdominal vein after tying off the right and here again I was unable to get the injection mass to pass through the veins of the kidney and enter the postcava. My results from the yellow

starch paste injection agree with those obtained by Lewis ('16) and disagree with those obtained by Robinson ('18) both of whom investigated the condition in the adult of this form.

In other specimens injections of a gelatin mass were carried out in the same manner as that used with the starch paste. The gelatin was colored with carmine or Berlin blue. These fluids never failed to pass through the veins of the kidneys and appear in the opposite vessel.

The results of these injections indicated that the vessels of the kidney are too small to permit the passage of the starch but that vessels do connect the renal portal vein with the postcava and that they are of capillary size.

By means of the celluloid corrosion method celluloid casts were made of the vessels of the kidneys. Some of these were made from single injections while others were made from double injections. In these injections a thin colored celluloid solution was used. In the single injections the fluid was injected into either the renal portal through the abdominal and external iliac or into the postcava. In either case, after corrosion or digestion there remained a cast of the vein with all its branches ultimately breaking up into capillary vessels, quite clearly demonstrating that no connection between the postcava and renal portal vein existed other than of a capillary size. The double injections were made by injecting two colors of thin celluloid, one color through the postcava and the other through the abdominal and external iliac into the renal portal vein. These casts were then carefully examined and dissected beneath the binocular microscope and invariably I was unable to find a single connection larger than capillary size.

For microscopical examination of the internal vascular structure a number of kidneys were injected with carmine gelatin through the left abdominal vein and an aqueous solution of Berlin blue through the aorta. A study of the serial sections of these injected specimens revealed the fact that no connections larger than capillaries were present between the branches of the renal portal vein and those of the postcava but that a capillary network with its glomeruli connections existed in which the branches of the postcava and renal portal vein ended, thus making a capillary system the only passage for blood between these two large trunks.

III. EMBRYOLOGY

The development of the renal portal system has been followed through a series of serially sectioned embryos of *Chrysemys marginata belli* and this supplemented by a study of injected embryos of the same species. The youngest embryo of the sectioned series measures 1.2 mm. in length and the oldest has a carapace length of 22 mm. The measurements of the younger embryos are crown rump measurements while those of the older embryos are measurements of the length of the carapace. In the present work the measurements referred to will be crown rump measurements unless carapace measurement is specified.

The outlines as shown in Figs. 1 to 6, Plate I, are outlines of the embryos whose reconstructed blood vessels are used for explanation in this work. The following table indicates the outline drawing, the length of the embryo and the reconstructions of its venous system.

OUTLINE FIGURE	LENGTH IN MM.	RECONSTRUCTION FIGURES
1	7	Plate II
2	10	Plate III
3	13	Plate IV
4	8 (carapace)	Plate V
5	12 (carapace)	Plate VI
6	22 (carapace)	Plate VII

The posterior cardinal veins first appear in an embryo of 4 mm. length. At this early stage these vessels open into the duct of Cuvier, continue posteriorly and gradually diminish in diameter. In the anterior portion they lie lateral to the mesonephric duct but shortly swing to a dorso-lateral position. At this time there are also noticeable disconnected venous islands formed ventral and mesial to the mesonephric duct. These islands are to be connected in the future to form the subcardinal veins.

An embryo of 7 mm. length (Plate II) has the posterior cardinal veins well developed anteriorly but posteriorly the vessels gradually reduce their diameter and are entirely wanting as a continuous vein in the extreme posterior region of the mesonephroi. However, the evidence of their future development in this region is indicated by several blood sinuses of considerable size. The posterior limb bud has at this time made its appearance, its drainage being cared for by the external iliac vein (V. E. I. D. and S.) which empties its blood into the posterior cardinal.

The future vertebral veins are also foreshadowed at this early

period by the development along their future path of a number of small blood sinuses.

The subcardinal veins follow rather closely the development of the posterior cardinal veins. Through anastomoses of the blood sinuses of the preceding stage a pair of venous channels or veins has been established. These vessels lie on the median ventral surface and in close relation to the mesonephroi. They eventually unite with each other and with the posterior cardinal veins. Even at this early stage there has been formed a few prominent unions between the posterior cardinals and the subcardinals (Plate II, Pc.Sc.A.). Not only has a connection been established between the larger portions of the veins, but at least one has been formed between two of the small portions which are as yet little more than blood sinuses. These anastomoses do not at this time penetrate the mesonephric substance but lie close upon the surface of that organ.

Anteriorly the posterior cardinals are beginning to show dorsal branches which later pass dorsal to the rib anlagen and usually bifurcate at this point, later becoming connected with each other through intermediate blood sinuses.

An embryo of 10 mm. length shows conditions as represented in Plate III. With the growth of the mesonephroi the posterior cardinal veins have reached a stage of completeness. Their position is dorsal and slightly lateral to the mesonephroi. The dorsal segmental branches of the posterior cardinals are fairly well established. The blood sinuses in the path of the future vertebral veins have by this time increased considerably in size and become more numerous. The subcardinal veins have rapidly developed into a pair of definite blood vessels lying ventral along the mesial edge of the mesonephroi, the right subcardinal vein being continued somewhat more anteriorly than the left.

A complete union of the subcardinal vessels has occurred just posterior to the omphalo-mesenteric artery by three large connections. There has also developed a free anastomosis between the posterior cardinal and the subcardinal vein of its respective side. These connections are for the most part situated on the periphery of the mesonephros, either on the dorso-median surface or the latero-ventral surface but appear to be in closer relation to the mesonephric tubules than in the previous stage. However, many of them do find their way between the tubules of that body.

At this stage in the development we find the caudal vein defi-

nately laid down. It bifurcates and each branch unites with the posterior portion of the subcardinal vein of its side. This arrangement establishes an embryonic renal portal system, the subelavian veins and caudal branches being the advent veins while the posterior cardinal veins function as the revehent veins.

With the further development of the mesonephroi, changes take place rapidly. The mesonephroi present a condensed appearance in the posterior region while the anterior portion is apparently beginning to atrophy. The posterior cardinals take up a more lateral position to the mesonephroi and greatly increase in size. The anastomoses between the posterior cardinal veins and the subcardinal veins, and between the two subcardinal veins increase extensively.

When the stage in development as represented by an embryo of 13 mm. length (Plate IV) is reached, the majority of the anastomosing connections no longer lie near the surface but dip deep into the mesonephric body sending venous pockets between the tubules. One of the most important developing structures during this period is the postcaval vein. The posterior portion of this vein develops from the subcardinal veins, chiefly the right. The development as found in this species duplicates that as found by Stromsten ('05) in *Kinosternon pennsylvanicum*.

The formation of the postcava which opens a new channel for the blood to reach the heart is accompanied by an important change in the embryonic renal portal system previously established. This change is completed by the change in position of the two branches of the caudal vein. These branches were previously connected with the posterior ends of the subcardinal veins. Through a shifting of the anastomosing connections between the subcardinals, postcardinals and caudal branches, the connection between the caudal branches and the subcardinal veins is lost and there is a connection established between the caudal branches and the posterior cardinal veins. With this new arrangement the blood is routed differently, the posterior cardinals and the caudal branches becoming the advent veins while the subcardinal veins and the postcava become the revehent veins.

The anterior portion of the vertebral vein has been completed at this age, being connected to the posterior cardinal vein by the dorsal segmental veins. The posterior region has not yet been formed but the process of development is under way as shown in Plate IV.

Following this stage in development there is a gradual approach toward the condition as found in the adult. The mesonephroi in the anterior region become more and more separated from the dorsal body wall. As development progresses they continue to degenerate in the anterior region while posteriorly they are large and compact.

This anterior degeneration of the mesonephroi is accompanied by the degeneration of the anterior region of the posterior cardinal veins and their dorsal segmental branches. A typical condition at this time is represented by reconstruction figures of Plate V made from an embryo measuring 8 mm. carapace length. The posterior cardinal veins still show the connections anteriorly in the regions of the subelavian vein but instead of a single large connection there are several small ones producing a network between the anterior end of the posterior cardinal vein and the duct of Cuvier. The degeneration process is quite apparent.

The degeneration of the anterior dorsal segmental branches is almost complete at this time, severing entirely the anterior portion of the vertebral vein and the anterior portion of the degenerating posterior cardinal vein. Posteriorly, the dorsal segmental branches, which have in the meantime developed, still persist, uniting the vertebral veins to the posterior portions of the posterior cardinals.

The posterior cardinals in the region of the mesonephroi are large and lie laterally within the periphery of these organs sending into the substance of the mesonephroi numerous small branches which anastomose freely with the remainder of the subcardinals or the posterior region of the postcava. This network at this stage is quite complex and represented in Plate V semidiagrammatically. Its character has been determined by a careful study of cross sections and longitudinal sections of injected embryos.

The mesonephros continues to become shorter and thicker due to the degeneration proceeding in the anterior portion. The splitting away from the dorsal body wall proceeds from anterior to posterior. At about this stage the metanephros appears as a dorsal outgrowth from the mesonephric duct, growing anteriorly and maintaining its position dorsally.

A general shortening of the renal portal system is in progress. The posterior cardinal veins lose their slight connection with the duct of Cuvier anteriorly and rapidly undergo degeneration in the anterior region (Plate VI). In the region of the largest por-

tion of the mesonephros and metanephros the posterior cardinal veins lie lateral to these organs and are quite large. Posteriorly these vessels diminish in size forming the posterior renal adhevent veins. The postcava has increased in size and the subcardinal anastomosis has not entirely disappeared. The mesonephric plexus has become still more complex and consists of much smaller blood passages than those in the previous stage. The dorsal segmental branches anterior to the fifth rib have all degenerated. Those posterior to the seventh rib have likewise degenerated leaving but two, one between the fifth and sixth ribs and one between the sixth and seventh ribs. The anterior portion of the vertebral vein is now entirely free from the posterior cardinal vein and is considerably larger than that lying posterior to the sixth rib.

The mesonephroi continue to degenerate from anterior to posterior and the metanephroi continue to develop from posterior to anterior, the two becoming about the same size in an embryo of 22 mm. carapace length (Plate VII).

The vertebral veins are completely formed at this time and receive the intercostal veins. The connection between the vertebral veins and the posterior cardinal veins lying between the sixth and seventh ribs as described in the embryo of a twelve millimeter carapace has now disappeared, leaving one large prominent connection between the fifth and sixth ribs.

The posterior cardinal veins have completely degenerated anterior to the mesonephroi and metanephroi. That portion of the posterior cardinal vein lying along the mesonephros becomes embedded between the mesonephros and the metanephros, giving branches to each of them. This is brought about by the fact that the vein lies along the dorsal surface of the mesonephros. The metanephros developing dorsal to the mesonephros gradually assumes a position dorsal to the vein so that the vein lies between the two. In addition to this vein as a blood supply there has resulted at this stage during the process of degeneration of the mesonephros a second and smaller vein, a branch of the embedded vein, which lies posteriorly along the lateral surface of the degenerating mesonephros. This vein I have termed the lateral mesonephric vein. With further development this vein disappears with the mesonephros.

The venous plexus of the metanephroi during this later period of growth is constantly becoming one of finer vessels as is shown by both stained and injected embryos.

Except for the portions of the subcardinal veins which enter into the formation of the posterior portion of the postcaval vein and metanephric venous plexus they entirely disappear. The changes taking place in the further development are not of great consequence. The mesonephros continues to degenerate until it disappears and the metanephros continues to develop until it reaches full size. The renal portal vein maintains its position and appears in the adult on the ventral surface of this organ. The larger veins of the venous plexus of the metanephros continue to be broken up into finer vessels until a complete capillary network exists between the renal portal vein and the posterior terminal branches of the postcaval vein. Thus there is established a true renal portal system, the advehent veins of which are the vertebrals, iliacs, renal portals and posterior advehentes, while the revehent vein is the postcava and its posterior terminal branches.

IV. DISCUSSION

In the embryology of the renal portal system of *Chrysemys marginata belli* there occurs the usual three important periods in structural development. There is a constructive period during which various structures are developed, a period of degeneration equally as important in respect to the final result, and a period of rearrangement and development of the organs functioning in the adult. These periods are not distinctly marked off from each other but one gradually merges into the other as the necessity for the change arises.

Due to the polarity of the embryo the anterior region develops first and remains in advance of the posterior region. Likewise any degeneration occurring originates in the anterior region and proceeds posteriorly.

The early formation of the anterior portion of the posterior cardinal veins seems to be shrouded in considerable doubt. The difficulty of following them during the earliest period of development has led to various ideas as to their origin. The prevailing idea of their origin is that advanced by Hoffmann, that they arise as longitudinal anastomoses between the intersegmental arteries. In view of the fact that I wish to deal with their later development and its influence in the establishment of a renal portal system I shall pass by this early stage of the formation of the anterior portion of these veins.

The studies of the posterior cardinal veins in Elasmobranch

embryos by Hoffmann, Balfour and Hochstetter agree quite closely, in so far as my observations go, with this form of Chelonia. In the Selachians these veins are found in early embryos to be two short veins lying closely beside the mesonephric duct and gradually growing posteriorly until they reach the full length of the mesonephroi. It is in much the same manner that they behave in the turtle. However, here I may add that the term "growth posteriorly" would be a general term since in reality a series of blood sinuses unites to form the posterior cardinal veins, the progress of the unions being from anterior to posterior. In an embryo of 7 mm. length these vessels have not yet been laid down the full length of the mesonephroi, but this condition is attained in an embryo of 10 mm. length.

According to Hochstetter ('88) in Selachians the subintestinal vein plays a conspicuous part in the formation of the renal portal system. In Chelonia another group of vessels is concerned in serving the same purpose as the subintestinal vein in Selachians. The shifting of the caudal vein branches and the posterior cardinal veins establishes a renal portal system in the adult Selachian. While this shifting of the caudal vein branches does occur in the turtles *Chrysemys marginata belli* and *Kinosternon pennsylvanicum*, the same structures are not affected in the Selachians as in the Chelonia. This is due to the fact that in the higher type of vertebrate, a new vessel, the post-cava, has arisen and functions in place of the anterior portions of the posterior cardinal veins which atrophy.

In *Chrysemys marginata belli* we find the Selachian stage of development of the renal portal system at its height when the mesonephroi, posterior cardinal veins, subcardinal veins and the caudal vein with its branches are functioning most efficiently. At this time the fact that a great change is imminent may be discerned by the presence of conspicuous vertebral blood sinuses and the initial formation of the dorsal segmental veins which appear to grow dorsally from the posterior cardinal veins.

For a comparison of the development of the veins of the renal portal system of this species of turtle with those of other Amniota we may turn our attention to the work of Rathke on snakes, Hoffmann and Hochstetter on lizards and Stromsten on turtles.

The posterior cardinal veins in *Chrysemys marginata* lying on the surface of the mesonephroi in early embryonic stages are apparently in sufficiently close relation to the mesonephric tissues

so that they can efficiently take care of these organs but with an increase in the volume of these bodies the veins must necessarily maintain their close association with the tubules. The surface of the growing mesonephros becomes somewhat rough due to the increase in number and size of the tubules. As a result, the posterior cardinal veins and subcardinal veins closely adhering to the surface become somewhat pocketed and these pockets extend inwardly between the mesonephric tubules. With continued growth of the mesonephroi the pockets increase in size and number and eventually those from the subcardinal unite with those from the posterior cardinal. The earliest unions of the pockets are formed on the dorsal and ventral surfaces of the mesonephroi so that a circulation is established between these two groups of veins. This arrangement is almost identical with that found by Lewis ('02) in the rabbit and probably corresponds with the intertubular vascular spaces of Minot. Later these connections penetrate the organs making a coarse network which with development is broken up into a finer network of capillaries (or sinusoids). The anterior portions of the posterior cardinals, in the region of their union with the duct of Cuvier, while originally large single vessels, break up later into several small venous connections (Plate V). This condition is due to the process of degeneration in this region.

The formation of the vertebral veins in *Chrysemys marginata* begins quite early. In fact there is indication of their formation as early as the 7 mm. stage. This is previous to the complete formation of either the posterior cardinal veins or the subcardinal veins and before a fusion exists between the subcardinals. There is already a chain of blood sinuses laid down in the position to be occupied by the vertebral vein. This early development of venous sinuses in turtles as anlagen for veins corresponds to the development of the posterior cardinals and subcardinals in birds as recorded by Miller ('03). In the early stages of the development of *Chrysemys marginata* the posterior cardinal veins, the subcardinal veins and the vertebral veins all show this primitive type of development. The vertebral vein originates as has been described, by the dorsal segmental branches passing dorsal to the anlagen of the ribs and through anastomoses with intervening blood sinuses. The formation of this vein is a progressive process beginning at the anterior end and proceeding posteriorly. This same method of origin, other than the inclusion of the blood sinuses, has been described by Stromsten ('05) in *Kinosternon pennsylvanicum* and by Kim-

ball ('23) for *Chrysemys marginata belli*. As has already been pointed out by Stromsten, the development of the vertebral veins in turtles differs from the development in the lizards, as recorded by Hochstetter, in that they develop dorsal to the rib anlagen in the former and ventral to them in the latter.

The subcardinals originally laid down as a series of anastomosing venous sinuses are well established in an embryo of 10 mm. length with a strong interanastomosis posterior to the omphalo-mesenteric artery (Plate III). These continue to develop and establish intimate connections between themselves and the posterior cardinal veins so that at the stage of 13 mm. length there exists a very extensive network of connections posterior to the omphalo-mesenteric artery, not only between the posterior cardinal veins and the subcardinal veins, but also between the two subcardinals. Since these connections are posterior to the omphalo-mesenteric artery there is no venous ring formed as described by Hochstetter in the development of *Lacerta agilis*. In regard to the dense network formed here, this agrees favorably with the lizards and with *Kinosternon pennsylvanicum*.

While the previous changes have been taking place, the branches of the caudal vein, through sinusoidal changes have had their connections with the subcardinal veins shifted to the postcardinal veins.

During these developmental stages the postcava has also begun to appear and has assumed a highly developed condition at the time the branches of the caudal vein shift from the subcardinal veins to the posterior cardinal veins. Among the animals possessing this vessel there is considerable variation in the method of its formation. This accounts for the various types of its expression in the adults. Goette in his work on *Bombinator igneus* describes the development of the posterior portion of the postcava as being formed by the union of the posterior cardinal veins which approach each other and fuse in this region. Balfour believes this to be incorrect since the Amniota as described by Rathke and others show no such process. In the lizard, *Lacerta viridis*, as described by Hochstetter, the extreme posterior portion of the postcava is formed from the two branches of the caudal vein and exists in the adult as a bifurcated vessel posteriorly. In *Chrysemys marginata belli* I find the development of its posterior region to wholly corroborate that as given by Stromsten for *Kinosternon pennsylvanicum*, that is, in this region it is formed by the "right subcardinal craniad of the

origin of the omphalo-mesenteric artery and the fused subcardinals caudad of this point."

When the development has reached this stage the degenerative factor assumes prominence. Previous to the formation of the postcava, the vertebral vein and the shifting of the caudal veins, the blood was carried from the caudal region by the caudal vein and through its branches was poured into the subcardinal veins. It then passed through the venous plexus of the mesonephros into the posterior cardinal veins which carried it anteriorly and discharged it into the ducts of Cuvier.

Now a new condition arises. The functioning of the postcava allows the blood to make a short cut to the heart. As a result of this, the posterior cardinal veins lose their connections with the ducts of Cuvier and degenerate. As found in lizards by Hochstetter this condition is accompanied by the separation of the anterior region of the mesonephroi from the dorsal body wall and the progressive degeneration of the mesonephroi and dorsal segmental veins. The posterior progressive degeneration of the mesonephros is probably aided by the development of the metanephros which appears at about this time (Plate VI). A rapid growth of the limb buds and the consequent relative reduction of the caudal region causes an increase in the size of the iliac vein and a reduction in importance of the posterior vertebral veins. This results in an enlargement of the iliac veins and a reduction in the size of the vertebral veins posterior to the kidneys. This progressive degeneration continues until the only connection remaining between the vertebral vein and the posterior region of the posterior cardinal vein is that as previously described lying between the fifth and sixth ribs. The portion of the posterior cardinal vein which fails to atrophy is that lying along the latero-ventral surface of the kidney and dorsal to the degenerating mesonephros. The lateral mesonephric vein is still present. The vein connecting the undegenerated portion of the posterior cardinal vein with the vertebral vein becomes the anterior renal advehent vein.

With this arrangement the blood flow is reversed. The blood now passes from the vertebral vein, the iliac vein and the caudal veins into the renal portal vein and from here through the venous network of the mesonephros and kidney into the postcava.

Degeneration of the mesonephros continues simultaneously with the growth of the kidneys. With the degeneration of the remain-

ing portion of the mesonephros the lateral mesonephric vein disappears leaving the vein lying ventro-lateral to the kidney as the only persisting part of the posterior cardinal vein. The kidney now takes the place of the mesonephros.

As the foregoing changes take place the venous network of the kidney becomes broken into more minute vessels until only a fine network exists. This network of capillaries (or sinusoids) has been tested as previously stated, by injections, by casts and by serial sections and in every case I find definite capillary connections (or sinusoids) which may be traced between the renal portal vein and branches of the postcava but in no case have I found a connection larger than capillary size.

This arrangement then produces a renal portal system in this form, the blood entering the kidney through the renal portal vein, traversing the capillary plexus of the kidney and leaving by the postcava.

V. SUMMARY

Previous workers have found a true renal portal system present in adult forms of fishes, Amphibians, lizards and snakes, but absent in birds and mammals. Occasionally suggestions have been made of the possibility of the transitional stages being found in the Chelonian group.

SELACHIANS

The early development of the renal portal system in *Chrysemys marginata belli* is fundamentally the same as the development of the renal portal system in the Selachians. The chief differences are that in Chelonia the postcava is substituted for the anterior portions of the posterior cardinal veins of the Selachians and the subcardinal veins in Chelonia are substituted for the subintestinal vein in Selachians.

The later development in Chelonia carries it far beyond the Selachian stage and agrees to a considerable extent with that as found in other reptiles and Amphibia, although several important differences in development appear.

AMPHIBIA

In Amphibia as described by Goette the posterior portion of the postcava is formed from the fused portions of the posterior cardinal veins while in Chelonia it is formed from the subcardinal veins.

LIZARDS

In lizards, the records of the earliest stages of development of the posterior cardinal veins and the subcardinal veins describe them as continuous connected blood vessels. The earliest stages of these vessels as observed in *Chrysemys marginata belli* show them to be discontinuous vessels with no connections.

The formation of venous pockets by the posterior cardinal and subcardinal veins is not described for lizards. These venous pockets are quite definite and distinct in this form of *Chelonia* and enter into the formation of the venous network of the mesonephros and metanephros.

The vertebral veins of the lizards develop ventral to the rib anlagen by anastomosing dorso-segmental branches.

The posterior portion of the postcava in lizards develops through anastomosis with the omphalo-mesenteric ring. In *Chelonia*, since there is no complete omphalo-mesenteric ring present it develops from a portion of the right subcardinal vein and the anterior region of the fused subcardinal veins.

SNAKES

In snakes the posterior portion of the postcava is developed as a bifurcated vessel while in *Chelonia* it is a single vessel in this region.

The posterior vertebral veins are prominent in the snake embryo and develop ventral to the rib anlagen. They finally disappear, leaving little or no trace in the adult while in *Chelonia* they remain as definite veins.

CHRYSEMYS MARGINATA BELLI (Gray)

1. The posterior portions of the posterior cardinal and subcardinal veins are formed by anastomosing blood sinuses.
2. The posterior cardinal and subcardinal veins become pocketed, these pockets lying between the mesonephric tubules.
3. The venous pockets unite to form venous connections between the posterior cardinal and subcardinal veins.
4. The subcardinal veins fuse posterior to the omphalo-mesenteric artery only.
5. The renal portal vein is the persisting portion of the posterior cardinal which lies between the mesonephros and metanephros.
6. The anterior renal advehent vein is the persisting dorso-segmental branch of the posterior cardinal which lies between the fifth and sixth ribs.

7. The vertebral vein develops from anastomosing branches of the dorso-segmental veins and intervening blood sinuses.

8. The connections formed by the union of the venous pockets of the posterior cardinal and subcardinal veins become broken up into a network of capillaries (or sinusoids) which persist and form an intra-renal network in the adult.

9. A true renal portal system is present in the adult form.

LITERATURE

Agassiz, Louis, 57. Contributions to the Natural History of the United States, Vol. II, Part III. Embryology of the Turtle; with thirty-four plates. Boston.

Balfour, F. M., 78. A Monograph on the Development of Elasmobranch Fishes.

81. A Treatise on Comparative Embryology, Vol. 11.

Gegenbauer, Carl. Elements of Comparative Anatomy. Trans. F. Jeffrey Bell.

Goette, Alexander, 75. Die Entwicklungsgeschichte der Unke.

Hertwig, O., 06. Handbuch der Vergleichenden und Experimentellen Entwicklungslehre der Wirbeltiere, Vol. III.

Hochstetter, F., 88. Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte des Venensystems der Amphibien und Fische. Morph. Jahrb., B. XIII.

88. Ueber den Einfluss der Entwicklung der bleibenden Nieren auf die Lage des Urnierenabschnittes der hinteren Cardinalvenen. Anat. Anz., B. III.

93. Beiträge zur Entwicklungsgeschichte des Venensystems der Amnioten. II. Reptilien. Morph. Jahrb., B. XIX.

Hoffman, C. K., 84. Beiträge zur Entwicklungsgeschichte der Reptilien. Zeitsch. f. Wiss. Zoologie, B. 40.

90. Bronn's Klassen und Ordnungen des Thierreichs, B. VI, Abth. III, Reptilien. Leipzig.

Hoffman, C. K., 93. Zur Entwicklungsgeschichte des Venensystems bei den Selachiern. Morph. Jahrb., B. XX.

Jourdain, S., 59. Sur le Systeme V. porte renale. Ann. des Sc. Nat., 4 Ser., T. XII.

Kimball, Pauline, 23. A Contribution to the Anatomy and the Development of the Arterial and Venous Systems in Turtles. The Anatomical Record, Vol. XXV.

Lewis, F. T., 02. The Development of the Vena Cava Inferior. American Journal of Anatomy, Vol. I.

04. The Question of Sinusoids. Anatomischer Anzeiger, Vol. XXV.

Miller, A. M., 03. The Development of the Postcava Vein in Birds. American Journal of Anatomy, Vol. II.

- Minot, Charles S., 98. On the Veins of the Wolffian Bodies in the Pig. Proc. Bost. Soc. of Nat. Hist., Vol. XXVIII.
00. On a hitherto unrecognized form of blood circulation without capillaries in the organs of Vertebrata. Proc. Bost. Soc. of Nat. Hist., Vol. XXXIX.
- Owen, Richard, 66. Anatomy of Vertebrates, Vol. I.
- Rathke, H., 39. Entwicklungsgeschichte der Natter. Königsberg.
48. Ueber die Entwicklung der Schildkröten. Braunschweig.
66. Untersuchungen über die Entwicklung und den Körperbau der Krokodile.
- Robinson Byron L., 18. Concerning the renal portal system in *Chrysemys marginata*. Anatomical Record, Vol. XIV.
- Schreiner, K. E., Ueber die Entwicklung der Amniotenniere. Zeitsch. f. Wiss. Zool., Bd. 71.
- Stromsten, F. A., '05. A Contribution to the Anatomy and Development of the Venous System of Chelonia. The American Journal of Anatomy, Vol. IV, No. 4.

PLATES

EXPLANATION OF PLATES

- Plate I. Outline drawings of embryos whose reconstructed veins appear in plates II-VII.
- Plate II. Frontal and right lateral reconstructions of the veins of an embryo 7 mm. long. (See Pl. I, Fig. 1).
- Plate III. Frontal and right lateral reconstructions of the veins of an embryo 10 mm. long. (See Pl. I, Fig. 2).
- Plate IV. Frontal and right lateral reconstruction of the veins of an embryo 13 mm. long. (See Pl. I, Fig. 3).
- Plate V. Frontal and right lateral reconstruction of the veins of an embryo 8 mm. carapace length. (See Pl. I, Fig. 4).
- Plate VI. Frontal and right lateral reconstruction of the veins of an embryo 12 mm. carapace length. (See Pl. I, Fig. 5).
- Plate VII. Frontal and right lateral reconstruction of the veins of an embryo 22 mm. carapace length. (See Pl. I, Fig. 6).

----- Outline of mesonephros.

----- Outline of metanephros.

Heavy horizontal lines indicate the level of the spinal ganglia.

- Ao. Aorta.
- Bl.S.Pe. Posterior cardinal blood sinuses.
- Bl.S.Sc. Subcardinal blood sinuses.
- Bl.S.V. Vertebral blood sinuses.
- D.C.D. Ductus Cuvier Dextra.
- D.C.S. Ductus Cuvier Sinistra.
- D.Seg.Br. Dorso-segmental branches.
- L.A. Longitudinal anastomosis.
- M.P. Mesonephric plexus.
- Pe.Sc.A. Posterior cardinal and subcardinal anastomosis.
- Se.Sc.A. Subcardinal and subcardinal anastomosis.
- V.Ac.D. Vein anterior cardinal dextra.
- V.Ac.S. Vein anterior cardinal sinistra
- V.C. Postcava.
- V.C.A. Postcava anastomosis.
- V.Ca.D. Vein caudalis dextra.
- V.Ca.S. Vein caudalis sinistra.
- V.D.Seg. Vein dorso segmental.
- V.Ext.J. Vein external jugular.
- V.I.E.D. Vein iliac externa dextra.
- V.I.E.S. Vein iliac externa sinistra.
- V.Int.J. Vein internal jugular.
- V.L.B.D. Vein limb bud dextra.
- V.L.B.S. Vein limb bud sinistra.
- V.Pe.D. Vein posterior cardinal dextra.
- V.Pe.S. Vein posterior cardinal sinistra.
- V.R.A.D. Vein revehens anterior dextra.
- V.R.A.S. Vein revehens anterior sinistra.
- V.R.P.D. Vein renal portal dextra.
- V.R.P.S. Vein renal portal sinistra.
- V.Sc.D. Vein subcardinal dextra.
- V.Sc.S. Vein subcardinal sinistra.
- V.Sbc.D. Vein subelavian dextra.
- V.V.D. Vein vertebral dextra.
- V.V.S. Vein vertebral sinistra.

PLATE I

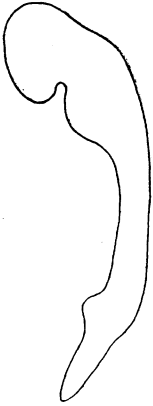


Fig 1

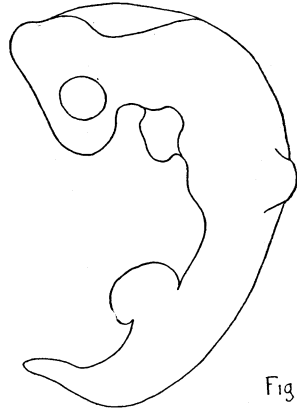


Fig 2

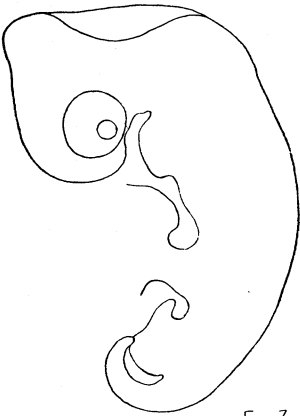


Fig 3

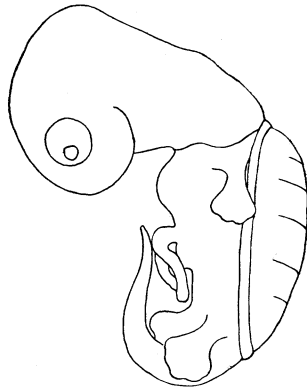


Fig 4

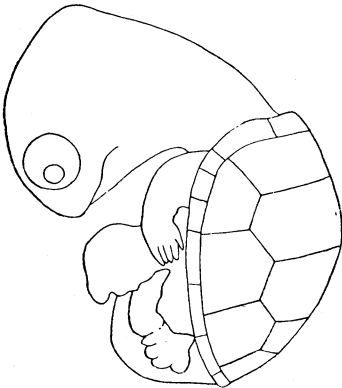


Fig 5

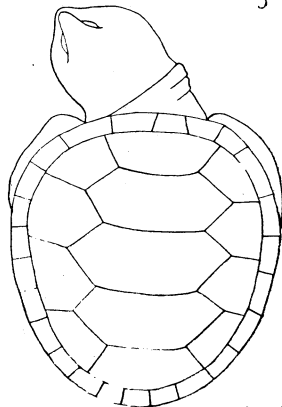
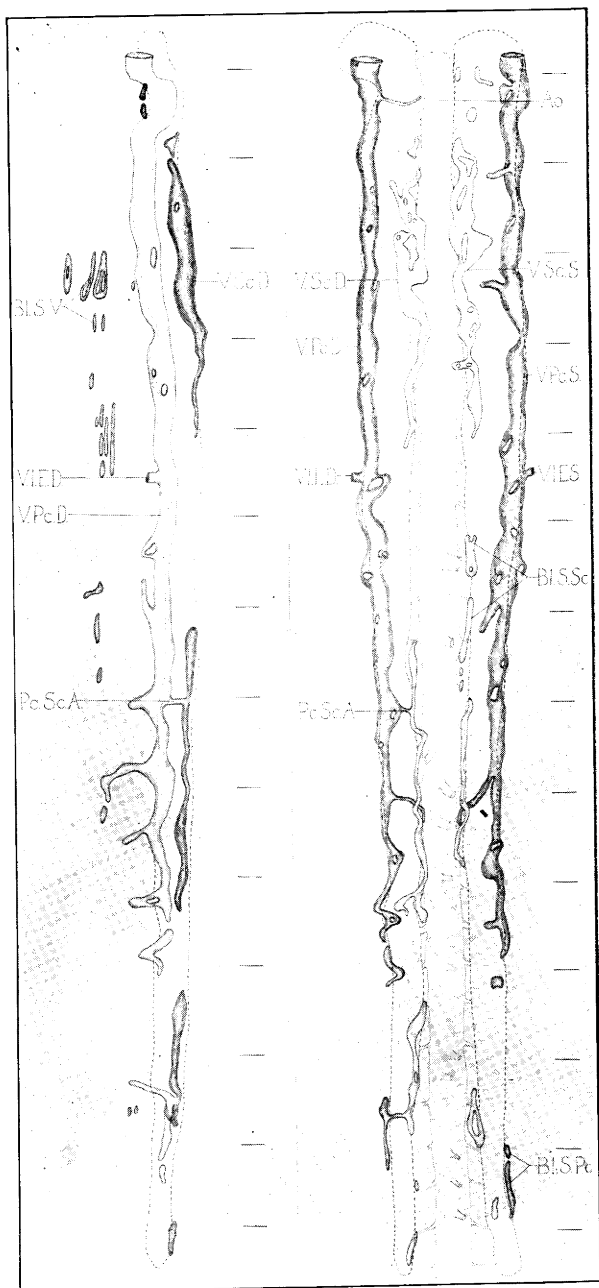


Fig 6



PLATE II



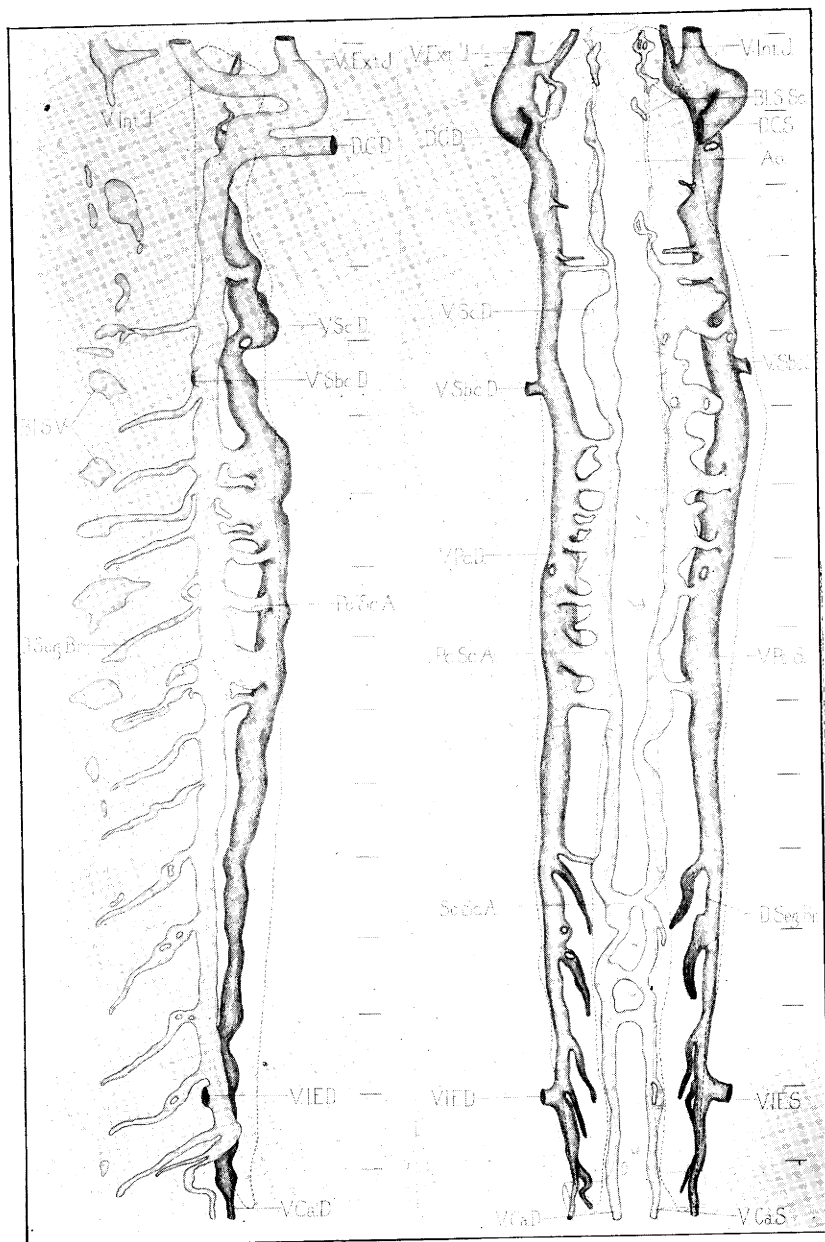
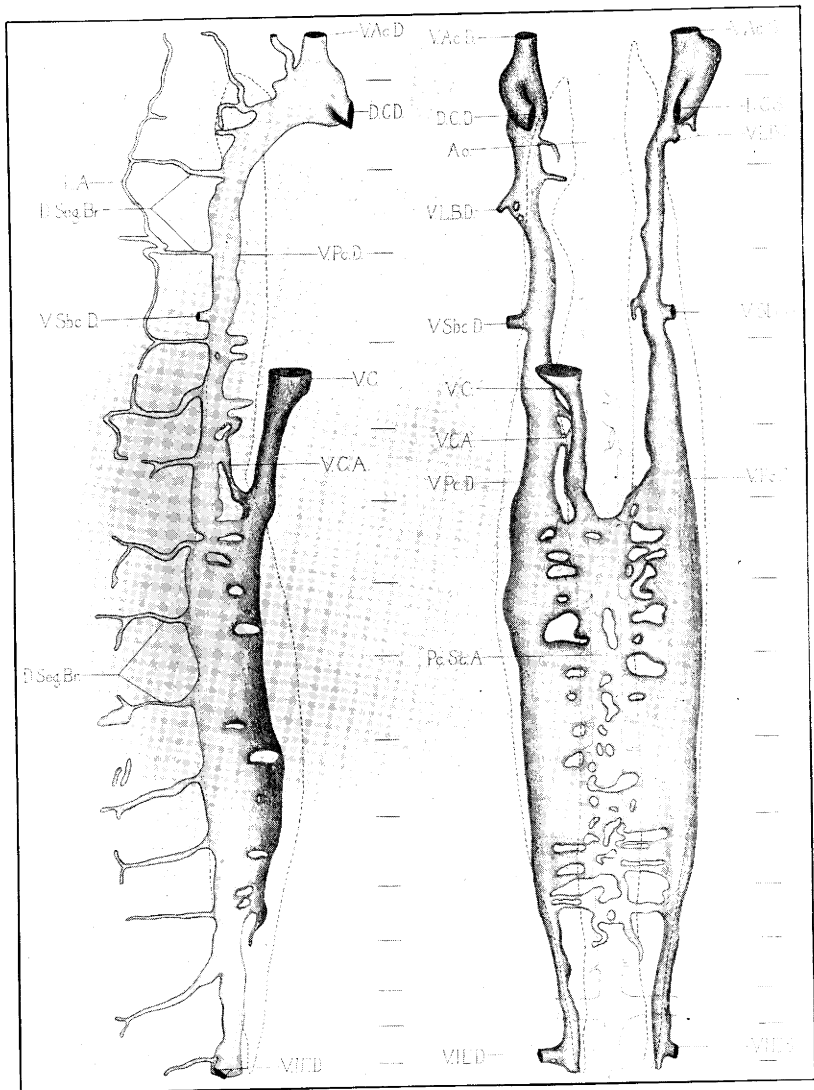


PLATE IV



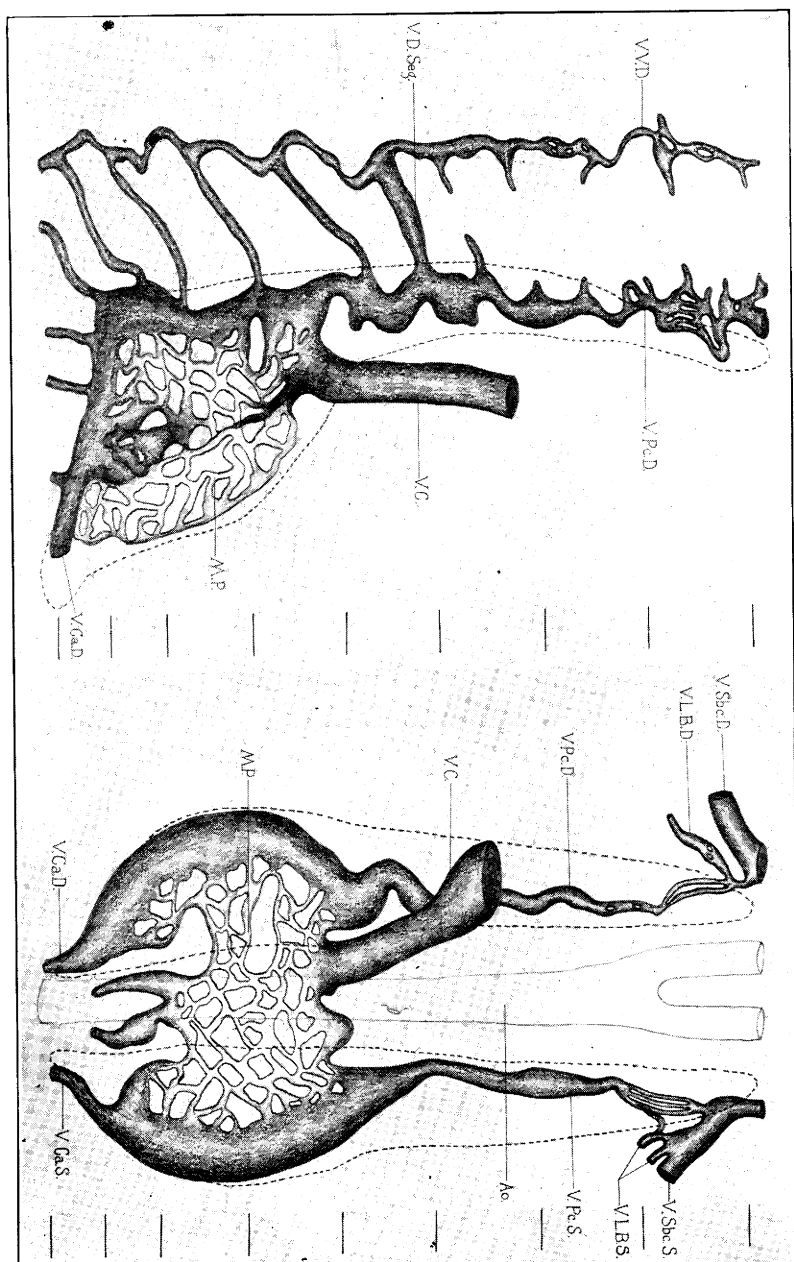


PLATE VI

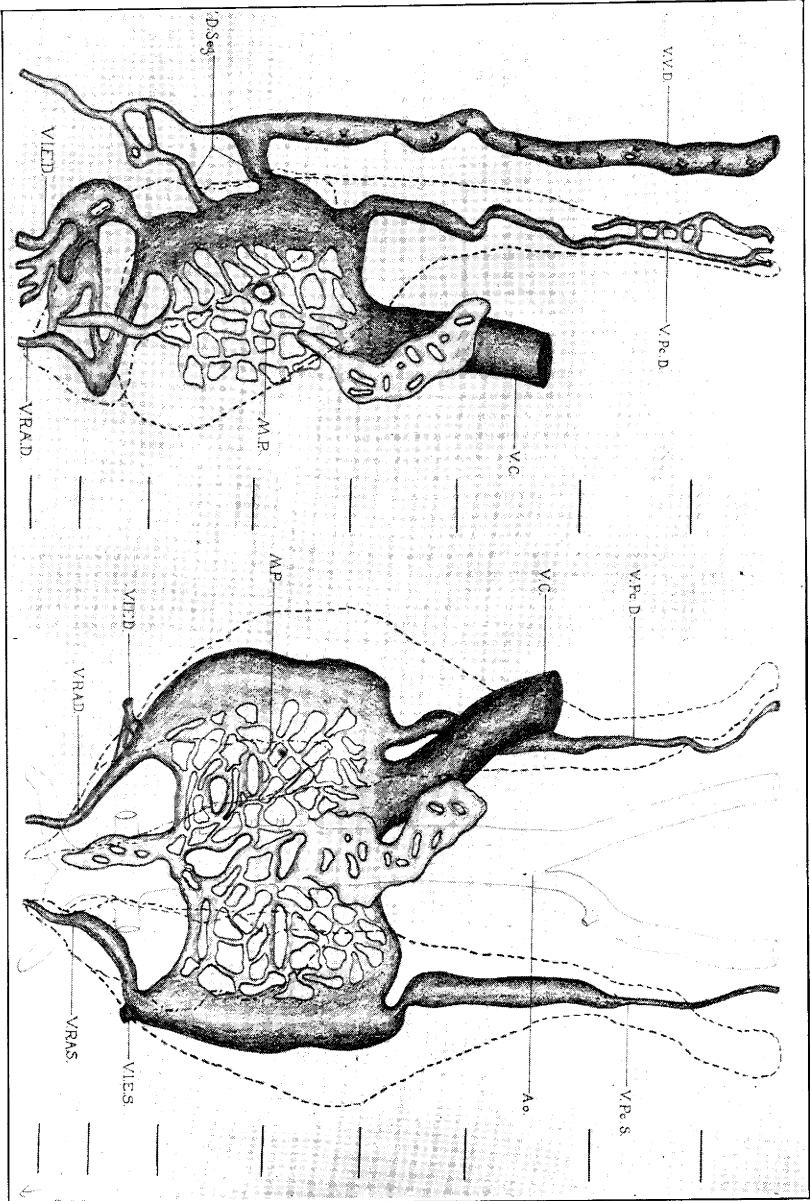
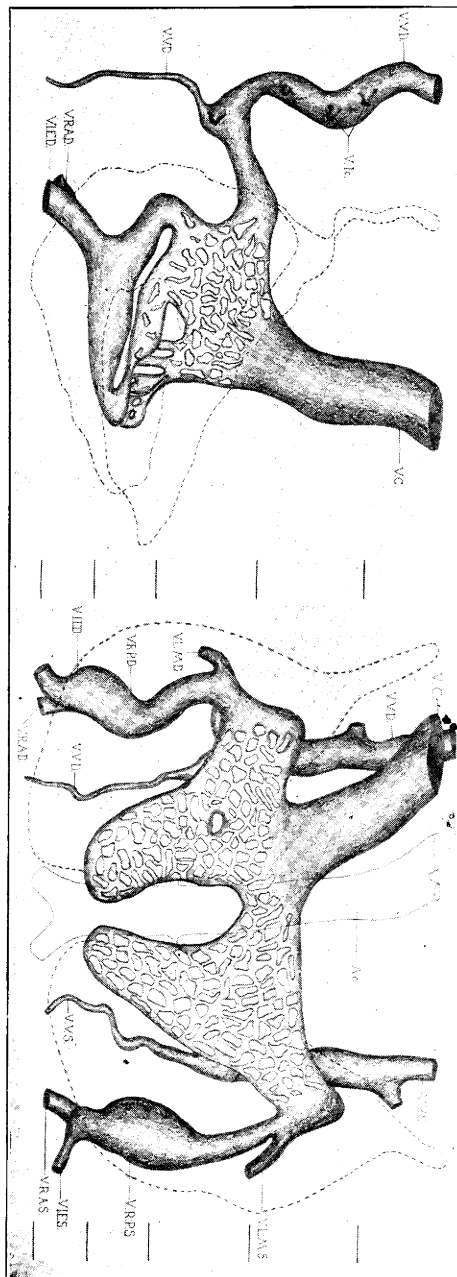


PLATE VII



UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

VOLUME XI

NUMBER 4

ENTOMOLOGICAL AND GEOLOGICAL PAPERS

PUBLISHED BY THE UNIVERSITY, IOWA CITY

Iowa Univ. Lib.
8-17-1925

CONTENTS

- Ants Collected by the University of Iowa Fiji-
New Zealand Expedition* W. M. MANN
- The Wasp-like Insects or Hymenoptera, Exclusive of Ants,
Collected by the Barbados-Antigua Expedition
from the University of Iowa in 1918* HENRY LORENZ VIERECK
- Tipulidæ Collected by the University of Iowa
Fiji-New Zealand Expedition* CHARLES P. ALEXANDER
- Photographic Practice for Field Geologists* CHESTER K. WENTWORTH
- The Desert Strip of West Molokai* CHESTER K. WENTWORTH

ANTS COLLECTED BY THE UNIVERSITY OF IOWA FIJI-NEW ZEALAND EXPEDITION

W. M. MANN

Bureau of Entomology, Department of Agriculture

Through the kindness of Professor Dayton Stoner, I have been able to examine the ants which he collected in New Zealand and in Fiji. In addition to new locality records for a number of the endemic Fijian forms, there is a new variety of *Rogeria* (*Irogera*) *tortuosa*, a description of which is included with the list of species.

NEW ZEALAND

Ponera antipodum Forel

Helensville.

Euponera (*Mesoponera*) *castanea* Mayr.

Auckland.

Monomorium (*Notomyrmex*) *antarcticum* F. Smith

Auckland; Helensville; Rotorua; Mt. Rangitoto.

FIJI

Odontomachus hæmatodes (Linné)

Suva; Viria; Walu Bay; Nukulau; Tamavua.

Cardiocondyla nuda (Mayr.)

Suva; Walu Bay.

Pheidole megacephala Fabr.

Suva. Several workers are among Professor Stoner's material.

In my paper on the ants of Fiji (Bull. Mus. Comp. Zool. Cambridge, Vol. LXIV, No. 5, p. 403) I stated that I had not taken *megacephala* in Lau and omitted to list it among the species of *Pheidole*. But on the larger islands, especially in the cultivated districts, it is one of the commonest ants.

Pheidole oceanica Mayr.

Circular Road, Suva. One worker.

Rogeria (*Irogera*) *tortuosa* Mann subsp. *stoneri*, new subspecies
Worker. Length 3.50 mm.

Differing from typical *tortuosa* in the absence of striæ on sides of occiput, in which character it resembles the subspecies *levifrons* and *polita* but is distinct from these as well as typical *tortuosa* in the structure of the epinotum, the base of which is longer and less convex and the superior spines broader, widely divergent and curved forward rather strongly instead of being straight as in the other forms of the species.

Type locality. — Tamavua, Suva.

Type. — In the museum of the State University of Iowa.

Cotypes. — Cat. No. 26487. U.S.N.M.

Described from two workers.

Tetramorium (Tetrogmus) simillimum (Mayr.)

Makaluva.

Tetramorium (Tetramorium) pacificum Mayr.

Suva; Walu Bay.

Tetramorium (Tetramorium) pacificum Mayr var. *wilsoni* Mann
Nukulau.

Tapinoma melanocephalum (Fabr.)

Nukulau.

Techomyrmex albipes F. Smith var. *vitiensis* Mann

Nukulau.

Plagiolepis longipes (Jerd.)

Suva; Makaluva; Nukulau.

Camponotus (Myrmogonia) laminatus Mayr.

Tamavua.

Camponotus (Myrmogonia) schmeltzii Mayr.

Suva.

Camponotus (Myrmoturba) maculatus (Fabr.) subsp. *pallidus*

F. Smith var.

Suva; Viria.

Camponotus (Colobopsis) dentata Mayr.

Makaluva.

Camponotus (Colobopsis?) vitiensis Mann

Tamavua. In Professor Stoner's material are five workers of this species, described originally from the mountains at Nadarivatu, and placed, with doubt, in the subgenus *Colobopsis*.

THE WASP-LIKE INSECTS OR HYMENOPTERA, EXCLUSIVE OF ANTS, COLLECTED BY THE BARBADOS-ANTIGUA EXPEDITION FROM THE UNIVERSITY OF IOWA IN 1918

HENRY LORENZ VIERECK
Ottawa, Ontario

Of the thirty-eight species of wasp-like insects, ants excepted, brought home from Barbados and Antigua by Dr. Dayton Stoner and submitted to me for study, I find that eleven are either new to subdivision 4 of the Neotropical Region or new to science.

LIST OF SPECIES

ICHNEUMONOIDEA

Vipionidæ

Apanteles (Apanteles) sp.

A single female that may represent a new species related to *A. (A.) levicoxis* Muesebeck, described from Utica, Mississippi. Antigua, July (Stoner).

Apanteles (Apanteles) sp.

A female and male presumably related to *A. (A.) ensiger* Say. Antigua, July 15-18 (D. & L. Stoner).

Apanteles (Protapanteles) sp.

One female that may prove to be the same as *A. (P.) floridanus* Muesebeck.

Antigua, July (Stoner).

Microbracon quintilis new species

Female. — Length 2.5 mm.; head above and thorax throughout as if covered with a brownish-yellow lacquer, face and mouth parts yellowish, excepting the blackish tips of the mandibles, antennæ 23-jointed, black or blackish, except for the apical and basal edges of the scape and pedicel which are more or less pale; tegulæ transparent, yellowish, wings infuscated, their veins blackish and yellowish, the costa between wing-base and stigma mostly yellowish, stigma yellowish with a blackish edge, legs, mostly, more or less

concolorous with the thorax, end joint of fore-tarsi and all joints of mid and hind-tarsi more or less brownish to blackish, hind tibiae yellowish except for the apical third which is more or less blackish; propodeum polished with a rudimentary median carina at apex; abdomen yellowish throughout, finely shagreened, almost sculptureless, first tergite with an inconspicuous apical carina, second tergite with an elongate impression on each side of the middle elevated area and with a sublateral impression nearer to the lateral margin than to the median impressions, apical margin of second tergite emarginate, sheaths of the ovipositor longer than the abdomen but shorter than the latter and the thorax combined, end sternite pointed and extending beyond the corresponding tergite.

Allotype — Essentially like the type but with the stigma darker and with the fourth, fifth and sixth tergites brownish black.

Related to *M. dorsator* var. *mellitor* Say.

Type and Allotype — Collection University of Iowa.

Type locality — Antigua, July (Stoner).

Microbracon sp.

One female related to the preceding and probably new to science. Antigua, July (Stoner).

Braconidæ

Bassus, n. sp.

Two female specimens, one broken.

Barbados, June 7 (D. Stoner); Antigua, July (Stoner).

Chelonus insularis Cress.

Many specimens. Antigua, July (Stoner).

Chelonus insularis Cress.

Variety with entirely black carapace. Six specimens. Antigua, July (Stoner).

Ichneumonidæ

Neopristomerus stoneri new species

Female. — Length 7 mm.; head and thorax mostly reddish; antennæ apparently a little longer than head and thorax combined, transfacial line : facial line :: 26 : 21, face and frons virtually equal in width, shining, closely punctured, clypeus yellowish, polished, sparsely punctured compared with the face, malar line apparently as long as the mandibles are wide at base, greatest diameter of lateral ocelli a little shorter than the ocellular line but apparently equal to the lateral ocellar line, temples shining, convex, apparently impunctate, vertex distinctly punctured, but sparsely; præscutum paler and more closely punctured than the parapsides, pronotum along the upper edge polished and sparsely punctured, elsewhere mostly shining and closely punctured, mesopleura and metapleura mostly densely punctured, veins and stigma mostly blackish, the latter apparently a little less than half as wide as long, legs yellowish to reddish except for the end joint of mid-tarsi, hind tibiae and

hind tarsi all of which are more or less brownish to blackish, denticles rudimentary between tooth and apex of hind femora, longer spur of hind tibiæ apparently more than one-third but less than one-half as long as hind basitarsus; propodeum sculptured much like metapleura, areola apparently twice as long as its greatest width, costulæ joining the longitudinal carina almost at the junction of the basal third of the areola with the apical two-thirds; abdomen polished or nearly so, mostly yellowish to brownish yellow, second tergite a little shorter than the first and together with the apical half of the first and the basal half of the third mostly black or blackish, basal half of the first tergite mostly stramineous, second tergite two and one-half times as long as wide at base, indefinitely longitudinally striate.

Presumably related to *N. melleus* Cushman.

Type — Collection University of Iowa.

Type locality — Antigua, July (Stoner).

Enicospilus purgatus Say.

Many specimens.

Antigua, June (Stoner). One ♂ specimen from the above lot and that may be a variety of *purgatus* goes to *neotropicus* Hooker in Hooker's key because it has only one corneous area in each wing.

CHALCIDOIDEA

Elachertidæ

Euplectrus sp.

Two females of what may prove to be a new species. Antigua, July (Stoner).

Pteromalidæ

Aplastomorpha? sp.

Determined by A. B. Gahan.

One male, Antigua, July (Stoner).

Cleonymidæ

Euchrysia buscki Ashm.

One female. Antigua, July (Stoner). Determined by A. B. Gahan.

Eurytomidæ

Decatomidea pallidicornis Ashm.

Two males that presumably belong to this species.

Antigua, July (Stoner).

Eucharidæ

Kapala sp.

One male that appears to be a new species was taken on Barbados, May (Stoner).

Chalcididae*Brachymeria ovata* Say

Three females. Antigua, July (Stoner).

Brachymeria robusta Cress.

One male and one female. Barbados, May, June (Stoner).

Spilochalcis flavopicta Cress.

Three females. Antigua, July (Stoner).

Spilochalcis femorata F.

Two females. Barbados, May (Stoner).

VESPOIDEA

Scoliidae*Compsomeris dorsata* F.

Six females and ten males. Barbados, Apr. 1914 (H. A. Bal-lou); May, June, July (Stoner); St. Kitts, Aug. 15, 1913 (Agr. Supt.).

Tiphia nitida Sm.

One female, two males. Spencers, Barbados, July 1911, June 1913, (Evely).

Psammocharidae*Psammochares (Pompiloides) coruscus* var. *juxta* Cress.

Female, Antigua, July 14-18.

Psammochares (Pompiloides) subargenteus Cress.

Antigua, July (Stoner).

Psammochares (Pycnopompilus) mundiformis Roh.

Male, Antigua, July 8, (L. Stoner).

Pepsis sanguigutta Christ.

Male, Antigua, June (D. Stoner).

Eumenidae*Odynerus (Ancistrocerus)* n. sp.

Female. Sandhurst, Nov. 22, 1905.

Odynerus (Pachodynerus) grenadensis Ashm.

Female. Sandhurst, Nov. 20, 1905.

Vespidæ*Polistes crinitus* Felton.

Females, Antigua, July 1, 8, 1918 (L. Stoner, Stoner). Deter-mined by S. A. Rohwer.

Polistes cincta Le P.

Females, Barbados, May 16-18 (D. & L. Stoner). Determined by S. A. Rohwer.

SPHECOIDEA

Sphecidae*Chlorion (Ammobia) ichneumoneum* L.

Male, Antigua, July (L. Stoner).

Notogonidea ignipennis Sm.

Male, Barbados, June (L. Stoner).

APOIDEA

Halictidae*Halictus (Chloralictus)* sp.

Female and two males, Antigua, July (L. Stoner).

Megachilidae*Megachile flavitarsata* Sm. var.

Male, Antigua, July 15-18 (D. Stoner). Appears to be a variety characterized by having black mid and hind-femora and tibiae instead of having those parts rufotestaceous.

Megachile concinna Sm.?

Male, Barbados, May 15-18 (D. Stoner).

Xylocopidae*Xylocopa fimbriata* L.

Female, Barbados, June (L. Stoner).

Euglossidae*Centris versicolor* F. race or var.

Female and male, Barbados, June (L. Stoner).

Apidae*Apis mellifera* L.

Workers, Antigua and Barbados (Stoner).

TIPULIDÆ COLLECTED BY THE UNIVERSITY OF IOWA FIJI-NEW ZEALAND EXPEDITION

CHARLES P. ALEXANDER
Amherst, Massachusetts

The crane-flies collected by the 1922 Expedition of the University of Iowa to Fiji and New Zealand have been submitted to the writer for determination through the kindness of Professor Dayton Stoner. The specimens, including the type of *Limonia stoneri*, have been returned to the University of Iowa. For convenience of treatment, the fauna of Fiji is considered separately from that of New Zealand, since there is no relation between the two.

FIJI

The crane-flies of the Fiji Islands are still imperfectly known, the only published papers upon them being two by the writer.¹ The fauna shows a marked endemism though clearly derived from the larger land masses lying directly to the eastward.

The present collection included three species of the tribe Limoniini, a group which is extremely abundant in number of species throughout the Oriental and Australasian Regions.

Genus DICRANOMYIA Stephens

1829. *Dicranomyia* Stephens; Cat. Brit. Ins., 2: 243.

Dicranomyia illingworthi Alexander

1914. *Dicranomyia illingworthi* Alexander, Ann. Ent. Soc. Amer., 7: 239-240.

This species was described from material taken at Nadi by Dr. James F. Illingworth. The present collection includes three specimens (1 ♂, 2 ♀) labelled "Fiji, June 1922." The species has more recently² been recorded from North Queensland.

¹ Alexander, Charles P. On a collection of crane-flies (Tipulidæ Diptera) from the Fiji Islands. Ann. Ent. Soc. America, 7: 239-246, pls. 34-35; 1914; New or little known Tipulidæ (Diptera).—VII. Australasian Species. Ann. Mag. Nat. Hist., (9) 8: 546-563; 1921.

² Alexander, Charles P. New or little-known Australian Crane-flies (Tipulidæ, Diptera). Proc. Roy. Soc. Queensland, 32: 92-109; 1920.

Subgenus THRYPTICOMYIA Skuse

1889. *Thrypticomyia* Skuse; Proc. Linn. Soc. N.S.W. (2) 4: 774.

Dicranomyia (*Thrypticomyia*) *subsaltens* Alexander

1922. *Dicranomyia* (*Thrypticomyia*) *subsaltens* Alexander; Ann. Mag. Nat. Hist., (9) 10:

This is the species that was earlier recorded as *Dicranomyia saltens* (Doleschall), from material taken by Dr. Illingworth at Nadi. Later material was received from Lautoka, collected by Messrs. Greenwood and Veitch. A study of this material revealed the specific distinctness of the species from *D. (T.) apicalis* (Wiedemann) which is now known to be distinct from *D. (Euglochina) saltens* (Doleschall) of the East Indian Islands. The present collection includes a ♂, Walu Bay, Suva, Viti Levu, June 13, 1922.

Genus LIMONIA Meigen

1803. *Limonia* Meigen; Illiger's Mag., 2: 262.

The center of distribution of the great genus *Limonia* appears to be the palæotropical region, from whence it has spread to almost all of the major land masses of the world. In the present collection, a single species was included which is herein considered as being undescribed.

Limonia stoneri, sp.n.

General coloration light yellow; pronotum darkened medially; head brownish black; legs yellow, the tips of the femora conspicuously blackened; abdominal tergites obscure brownish yellow, each with a transverse central band of dark brown, sternites dark brown.

Female.—Length about 10 mm. Described from an alcoholic specimen.

Rostrum brown; palpi dark brown. Antennæ with the scape dark brown; flagellum paler brown, the basal segments with the proximal portion yellowish. Head brownish black.

Pronotum yellow, dark brownish medially. Mesonotal præscutum and scutum yellowish, the former very narrowly and indistinctly darkened anteriorly; scutellum light yellow with a small brown spot on either side of the median line at the base; postnotum yellow, the basal median region more or less darkened. Pleura yellow. Halteres yellow, the knobs dark brown. Legs with the coxæ and trochanters yellow; femora yellow, the tips rather broadly and conspicuously blackened; tibiæ obscure yellow, the tips very narrowly darkened; tarsi obscure yellow. Wings badly injured and their characters can be defined in general terms only; general coloration pale brown, the costal region more yellowish; stigma relatively small, oval, dark brown; veins dark brown, those in the costal region more yellowish. Venation: *Sc* long, *Sc*₁ alone a little longer than the distance between the tip of *Sc*₁ and the proximal end of *Rs*.

Abdominal tergites obscure brownish yellow, with a transverse central band of dark brown across each segment; the pale apex of each segment is a little broader than the similarly colored apex; subterminal segments light yellow; sternites dark brown, the subterminal segments yellow. Ovipositor with the tergal valves relatively short and slender, the longer, straight sternal valves blackened at base.

Habitat. — Fiji (Viti Levu).

Holotype, ♀, Walu Bay, Suva, June 13, 1922 (Dayton Stoner).

The type of this interesting species is in the University of Iowa. It is named in honor of the collector, Professor Dayton Stoner.

NEW ZEALAND

The crane-fly fauna of New Zealand is now known to be an extremely rich and varied one. At the time of the signing of the armistice in 1918, the total number of species of Tipuloidea described from New Zealand was less than fifty. Since that time there has been great activity among collectors and a very considerable number of additional species have been described, chiefly by Edwards and the writer. The number of species now known from New Zealand is not less than 350 and the number will be still further augmented with additional collections. The present collection includes only 9 species but this must be considered as being a fair representation of the fauna on the wing at the time the collections were made. The published records for Auckland are very poor and the present list adds several species to the list from this Province.

Genus DICRANOMYIA Stephens

Dicranomyia ægotans Edwards

1923. *Dicranomyia ægotans* Edwards; Trans. N.Z. Inst., for 1921, 54:

Two ♂♂ from Kauri Gully, Auckland, July 18, 1922. The species has a very wide range throughout both islands of New Zealand.

Dicranomyia vicarians (Schiner)

1868. *Limnobia vicarians* Schiner; Novara Reise, Dipt., p. 46.

This is one of the commonest and best-known crane-flies in New Zealand, ranging over most of both islands. The present collection includes a specimen from "The Domain," Auckland, July 14, 1922.

Dicranomyia nephelodes Alexander

1922. *Dicranomyia nephelodes* Alexander; Ann. Mag. Nat. Hist., (9) 10: 84-85.

This recently described crane-fly has been known only from the vicinity of Ohakune, at the foot of Mount Ruapehu, where the types were taken by Mr. Harris. The present collection includes material from Kauri Gully, Auckland, taken July 15-18, 1922.

Dicranomyia cubitalis Edwards

1923. *Dicranomyia cubitalis* Edwards; Trans. N.Z. Inst., for 1921; 54:

This is another widely distributed species, occurring in both islands. The present collection includes material from Kauri Gully, Auckland, July 15, 1922.

Genus *MOLOPHILUS* Curtis

1833. *Molophilus* Curtis; Brit. Ent., p. 444.

The genus *Molophilus* is one of the largest genera in New Zealand, where the number of known species is not far from fifty.

Molophilus multicinctus Edwards

1923. *Molophilus multicinctus* Edwards; Trans., N.Z. Inst., for 1921; 54:

A specimen from Helensville, Auckland, July 17, 1922. The fly has a wide range in both islands.

Molophilus aucklandicus Alexander

1923. *Molophilus aucklandicus* Alexander; Ann. Mag. Nat. Hist., (9) 10:

This species was described from Auckland, based upon material taken by Mr. Harris. The present collection includes a ♂ from Kauri Gully, Auckland, July 18, 1922.

Genus *AMPHINEURUS* Skuse

1889. *Amphineurus* Skuse; Proc. Linn. Soc. N.S.W., (2) 4: 802.

This large and important genus reaches its maximum of specific development in New Zealand. It is unquestionably allied to *Ormosia* of the Northern Hemisphere but must be considered as being distinct.

Amphineurus perdecorus Edwards

1923. *Amphineurus perdecorus* Edwards; Trans. N.Z. Inst., for 1921, 54:

One ♂ from Kauri Gully, Auckland, July 18, 1922. This rather uncommon crane-fly occurs in the North Island.

Amphineurus, sp., near *gracilisentis* Alexander

1922. *Amphineurus gracilisentis* Alexander; Ann. Mag. Nat. Hist., (9) 10: 563.

A large female specimen from Kauri Gully, Auckland, taken

July 15, 1922, may belong here. It is not possible to determine isolated females in many of the larger genera of Tipulidæ.

Genus TRIMICRA Osten Sacken

1861. *Trimicra* Osten Sacken; Proc. Acad. Nat. Sci. Phila., p. 290.

The genus *Trimicra* occurs on virtually all of the continents and many of the oceanic islands. There is still much doubt as to how many species are involved but the present evidence seems to indicate that virtually all of the many described species are synonymous with the first-described *T. pilipes* (Fabricius). Considerable variation in the length of the 2nd anal vein in these various so-called species makes it necessary to investigate certain of them more closely, since this character of length of the 2nd anal vein has been used as a generic and subgeneric criterion in other groups of the Eriopterini.

Trimicra inconstans Alexander

1922. *Trimicra inconstans* Alexander; Ann. Mag. Nat. Hist., (9) 9: 148, 149.

Several specimens from Helensville, July 17, 1922; one ♂ from Rotorua, vicinity of hot springs, July 31, 1922. This latter has been recorded by Professor Stoner ³ as feeding on the algæ growing on the hot sand in the near vicinity of the hot, bubbling springs.

³ Stoner, Dayton. Insects taken at Hot Springs, New Zealand. Ent. News, 34: 88-90; 1923.

PHOTOGRAPHIC PRACTICE FOR FIELD GEOLOGISTS

CHESTER K. WENTWORTH
University of Iowa

INTRODUCTION

FOREWORD

In preparing the following paper the writer has received suggestions and criticism from a number of geologists and students of photography. Considerable difference of opinion existed among those who read the preliminary manuscript in regard to the desired emphasis on different points and on the length of treatment but in general suggestions made were followed in revising the paper. Especial thanks are due to R. B. Wylie, J. J. Runner, and E. T. Apfel of the University of Iowa, to F. E. Wright of the Geophysical Laboratory at Washington, and to E. A. Shuster of the Photographic Laboratory of the U. S. Geological Survey for helpful comments and criticism.

PURPOSE OF GEOLOGICAL PHOTOGRAPHY

There are two general classes of photography: the one, which may be designated as artistic photography, being practiced primarily for esthetic purposes; the other, known as record photography, being devoted to practical ends in the pure and applied sciences. Photography as practiced by geologists belongs essentially to the latter class and it is in the main from the practical standpoint that it is considered here. Photographs are used in the presentation of the facts and principles of geology. These may be presented as a part of an original contribution to the science or they may be presented as parts of a treatise representing current knowledge in one or all branches of the subject. In either case the photographs may accompany a printed book or paper or may be copied in the form of lantern-slides or prints to illustrate an oral discourse. More frequently than otherwise the use of photographs renders the presentation not only more pleasing but also effects a considerable

economy of time and space. In the case of most sorts of bare facts the effectiveness of presentation is probably greatest when the phenomena are actually seen by the person who is to be informed. Next in order is the viewing of a good picture and third and least effective as a single means is the text description. A combination of the latter two is probably more effective than either alone and next best to the combination of observation and discussion of the phenomena at first hand. In addition to their use as single permanent records photographs are sometimes of great value to show progressive changes such as those which take place in vegetation, processes of erosion or deposition and the like and are then taken in series.

IMPORTANCE TO FIELD GEOLOGISTS

The importance of a knowledge of photography to field geologists is apparent when it is recognized that, except for the most general views of topographic features and for photographs of common features which may be recognized by inspection, the great bulk of photographs of value in geologic investigations or teaching must be taken by the geologist most familiar with the phenomena to be illustrated. It is the exception rather than the rule when it is possible for the geologist to designate the features of importance and have them photographed by a professional photographer. Not only must the field investigator himself determine the features of which pictures are to be made but he must decide upon the point of view, the arrangement if they are movable, and the other conditions so far as they may be controlled and he alone is able satisfactorily to decide upon the fitness of the resulting pictures. It is true that that part of the picture making which may be called the dark-room technique may be advantageously turned over to others. It is very desirable, however, that the geologist be versed in the general principles of developing and fixing of negatives and of making prints for he can then most intelligently recognize the sources of imperfection in resulting pictures and improve his own technique or criticise that of the dark-room as the case may be. Consideration of the dark-room technique is beyond the scope of this paper and moreover is adequately treated in an extensive literature since that of use to geologists is no different from that of other branches of record photography.

In the case of field procedures, however, there seems to be room

for description of the methods and equipment which have been found most useful. Much that appears below is applicable to other branches of out-of-door record work such as that done by students of botany, zoology and other branches of natural science.

DIVERSITY OF PHOTOGRAPHIC CONDITIONS IN THE FIELD

If field photography may be said to have any essential peculiarity it is the extreme diversity of conditions which are confronted. These include variations of sunlight due to differences of time of day and condition of the atmosphere as well as those due to differences in latitude and season of the year. Subjects vary enormously in their colors, inherent contrasts and brightness. Many of these are quite fixed and immovable and are in positions none too favorable for successful photography. Even in those cases where the subjects might more advantageously be photographed under better conditions of light or at another time of day it is not commonly practicable for the field geologist to wait for the improved conditions. The observation, note-taking, collecting and other operations of field investigation are so onerous that most commonly the geologist will not have occasion to return to the exact spot and should be prepared to secure the best possible results in photography at the time he first studies any given feature.

LIMITATIONS IN EQUIPMENT ¹

The geologist's task is made more exacting by the fact that he can usually carry but a limited amount of equipment, a considerable part of which is for other than photographic purposes. With the very restricted amount of photographic equipment at hand he must photograph a wide range of subjects under conditions far more diverse than those met by most commercial photographers. It is clear that success in this work demands considerable knowledge of photographic principles and careful choice of equipment as well as painstaking attention at all times to the technical details.

EQUIPMENT FOR FIELD USE

THE CAMERA

The writer does not propose to discuss the relative merits of many different models of domestic and foreign hand cameras which

¹ It has seemed best in the present paper to treat the subject of field

are available. It will be sufficient to point out the inherent advantages and disadvantages of a few types as related to different sorts of field photography. Cameras of interest to field geologists may be grouped in four classes. These are

1. Roll film folding cameras
2. Plate back folding cameras
3. View cameras with long extension
4. Reflecting cameras

Perhaps the first choice to be made is that between roll film cameras and plate-film pack cameras. The former are unquestionably more convenient to manipulate and carry and the roll films are more readily obtained in small towns than plates, cut films or film packs. The roll films are far lighter per exposure than plates or cut films and the roll film camera is somewhat less bulky than the plate camera of the same nominal size. For the geologist who wishes to do critical work in both detail and distant views the plate camera has certain distinct advantages among which are the use of the ground glass for focusing and composition, the use of various grades of films or plates such as those of varying speed, contrast or color sensitivity.

The ultimate choice between the roll film and plate cameras depends on the personal attitude of the user toward photography. Not all aspects of field technique will be accorded equal attention by different persons and by some photography will be treated as a necessary part of the field work but not as an avocation as it will by others. For the geologist who wishes to cope with the unusual and difficult subjects and to use different grades of cut films and a convertible lens the plate camera is essential. On the other hand, using the same care on the details, negatives of equal quality can probably be made from four out of five subjects with the roll film type of folding camera. The scope of this sort may be greatly increased by the use of auxiliary lenses as previously described by the writer.¹

There are opportunities for a considerable range of choice in selecting a roll film camera and it is sufficient to point out that a brilliant view finder, rising and falling front, substantial bed

photography from the standpoint of travel on foot. Travel by automobile where it is practicable permits transportation of more elaborate equipment but the same principles hold in the field practice.

¹ Wentworth, C. K. (Adapting a Short Bellows, Roll Film Camera for Detail Work.) *Journal of Geology*, Vol. XXX, pp. 158-161, 1922.

and focusing mechanism and a dependable shutter are the important features. There is an even greater diversity of type in plate cameras. Box cameras of the Corona type are very useful for all kinds of out of door work close to headquarters or when working by automobile but are, even size for size, rather bulkier than other types and are not so convenient for foot travel. There are a number of small plate-back folding cameras, especially in the foreign makes, which have longer bellows extension to facilitate short range focusing and the use of single components of convertible lenses. These are very useful in combining portability with the advantages of ground glass composition and use of various grades of plates or films.

Reflecting cameras of which the Graflex may be taken as a type are unexcelled for photographing moving objects or those that must be caught in certain transitory positions. Some of them are fitted with long bellows extension and other adjustments and when used with a tripod are equally satisfactory for still pictures. The mechanism throughout is usually high grade and for general purposes they must rank high. At the same time they are necessarily heavy and bulky and will hardly be chosen by the geologist who must carry his equipment on foot. For most geologic pictures speed is not essential and the shallowness of definition forced by the use of wide apertures is so objectionable as to be justified only where the speed is absolutely necessary. In all other cases the extra weight of the Graflex which is aimed mainly at this one object serves no purpose.

In choosing a camera for every day field use perhaps the first question to be considered is size. Probably the bulk of pictures taken for geologic illustration are made with cameras of the $3\frac{1}{4}'' \times 4\frac{1}{4}''$ or $3\frac{1}{4}'' \times 5\frac{1}{2}''$ sizes. The writer believes that one or the other of these sizes will be found more satisfactory than any larger or smaller sizes. Much has been written on the general plan of making sharply defined small negatives with a high grade anastigmat lens and enlarging the image in printing. Theoretically the plan has much to commend it. Equipment is much lighter and less bulky, the short focus lens has greater relative depth, film is less expensive and easier to store than in the larger sizes. Satisfactory enlargements for ordinary pictorial purposes can undoubtedly be made from small negatives for purposes of scientific record. However there are so many sources of defective

definition or of other flaws in the negative that the writer believes in the long run the average negative is none too good and should be large enough to give by contact printing an image of sufficient size to serve as a moderate sized illustration in a published paper or large enough to serve as a lantern slide for projection. The labor and expense of printing by enlargement is considerably greater than that by contact and the writer does not know of a single geologist who possesses an extended series of good field pictures made wholly by enlargement from the negatives.

THE LENS

There is a wide range of choice in lenses. A lens at least as good as the widely known Rapid Rectilinear is essential. For a few geologic subjects greater speed than is given by the $f/8$ aperture is needed. It is a source of much satisfaction to have a high grade anastigmat lens for these occasional needs but the writer believes the desirability of a fast lens can be greatly exaggerated. It seems to him profoundly true that a fine series of photographs illustrating geologic features reflects patience and skill on the part of the photographer to an enormously greater degree than it does the quality of the lens he used. From inspection of most such pictures it is quite impossible for anyone to tell with what sort of lens they were taken and compliments on ones lens based on admiration of good photographs of the features ordinarily taken by geologists commonly indicate only ignorance of the most elementary photographic principles. By the foregoing statement the writer has no intention of appearing scornful toward high grade lenses but merely wishes to emphasize the view that understanding of the equipment the operator has in hand is of vastly more importance than the price he paid for it.

There is so much popular misunderstanding on the subject of lenses that a few words on elementary principles will not be amiss at this point. A simple meniscus lens such as that of a small pocket magnifier has six principal types of defect or departure from perfect definition. There are spherical aberration, chromatic aberration, distortion, curvature of field, astigmatism and coma. These may be briefly defined as follows:

Spherical aberration — Caused by the convergence of rays passing through the outer parts of the lens at different distances from those passing through the central parts.

Chromatic aberration — Caused by the convergence at different distances of rays of different colors, hence of different wave lengths.

Distortion — Caused by convergence of rays from objects not on the lens axis at distances from the axis not strictly proportional to the distances of the objects from the axis. Straight lines not passing through the center of the field become slightly curved in the image.

Curvature of field — Consists in the convergence of rays from outer points of a plane field at different distances from those from the central parts, thus making the focal locus a curved surface symmetrical to the lens axis rather than a plane.

Astigmatism — Consists in the establishment at different distances of images of lines radial to the lens and those tangential to the lens.

Coma — Consists of a blur produced by lateral spherical aberration of rays passing obliquely to the axis of the lens.

In high grade lenses these defects are greatly reduced in amount by the combination of simple lenses of different forms and made of glass of different refractive and dispersive qualities but they are never completely eliminated. All these defects are much reduced in actual practice by using small apertures.

The six defects mentioned above are so interrelated that an attempt to achieve partial perfection by the elimination of any one usually results in increasing one or more of the others. For any lens the so-called speed (a most misleading term) or relative aperture is the ratio between the largest aperture at which the lens will give satisfactory definition and its focal length. Satisfactory definition is commonly considered to exist when the image of no point is dispersed by the combined defects over a circle of greater than $1/200$ inch in diameter. Most lenses are so mounted that no larger apertures may be used and the "speed" is thus a statement of the largest working aperture. There is no practical difference in the rate at which light passes through the glass of different lenses nor in the amount of light transmitted by an aperture of unit size.

Depth of definition is not an inherent quality of a lens. It is a variable condition controlled by the aperture in use and the focus of the lens and is the same for all lenses of the same focus and at the same aperture. The very great and very useful depth

of definition of fixed focus cameras of the Brownie type is a necessary consequence of their small maximum apertures and relatively short focus and may be duplicated by using proper adjustments on any small hand camera.

A convertible lens is one so designed that one of the two components may be used alone. In some lenses the two components are identical and either may be used with the same result; in others known as triple convertible the two components are of different focal lengths and thus by using either alone or the two together offer three focal lengths. The advantage of the choice of focal lengths is very great in controlling the size of the image when the viewpoint is fixed by topographic or other conditions. The longer focal lengths give larger images from a fixed viewpoint and have the quality of giving less pronounced perspective than the shorter focal lengths.

Very short exposures are not essential for most geologic subjects since these are stationary and excessively large apertures are undesirable because of the shallowness of definition. The writer feels that a lens of $f/6.3$ aperture and possessed of low distortion and curvature of field is as good as any for field use.

An excellent description of many of the well known types of lenses is contained in the article on Photography in the *Encyclopedia Britannica*, 11th Edition.

Closely related to the question of lenses is that of shutters. Lenses of larger apertures than $f/8$ are commonly fitted with shutters in which a spring previously set is released by the trigger whereas those of $f/8$ and less, commonly have the energy furnished and release effected by the same movement of the hand. When the former type is used in the field the writer believes quite as much benefit is derived from the advantage of the compound shutter as from the superior lens. The latter type of shutter rarely has actually the speeds nor the range indicated, the high speeds being slower and the lower speeds faster than those shown. The former type, if in good condition, is far more likely to show close agreement between indicated and actual speeds and furthermore is susceptible of more accurate adjustment. The focal plane shutter is indispensable for cameras of the Graflex type but as mentioned above these are not considered to be so convenient for general geologic work.

There are various accessory devices which have been developed

by various makers, some of which are essential and others of less value. The rising and sliding front is valuable and will be found on most cameras having other necessary features. The writer has made little personal use of the autographic features since he prefers to add photographic notes to others constantly made in the field note books but other geologists prize the feature highly. The range finder with which some cameras are equipped is probably of less value to the geologist than to the general public since he probably estimates distances with considerable accuracy by inspection. The same may be said of a level. The writer finds that sighting on the horizon or comparison with the vertical lines of trees insures reasonable alignment of the pictures for ordinary purposes. The use of a precise level for phototopographic work of any sort is of course quite another matter.

PLATES AND FILMS

There is a wide variety of plates and films of various makes available at the present time, of which practically all may be regarded as of excellent quality. Roll films and film packs are commonly of one speed and orthochromatic to a moderate degree. Some of the film of film packs appears to carry a slightly thinner emulsion than the roll film but this difference is of relatively small importance on most subjects. Glass plates in all the standard sizes may be had in a number of speeds and degrees of contrast and with orthochromatic and panchromatic color-sensitive emulsions. A similar variety is available in the newer cut films which are extensively used by many commercial and amateur photographers. The principal advantage of the cut film over the plates aside from the obvious reduction of weight and danger of breaking is that in the film halation is practically negligible due to the lesser thickness and reduced reflections.

A few general principles may be noted here. Very rapid plates or films commonly have somewhat coarser grain in the emulsion and also have considerably less latitude. The slow process plates have likewise much less latitude. Where special purpose films or plates are needed they serve admirably but it must be remembered that in many instances their special properties have been secured at the sacrifice of some other feature. Color-sensitive plates and films have revolutionized the photography of certain objects and will undoubtedly increase in use in the future. In conjunction

with the proper filters they permit the portrayal of any object in terms of a small part of the total light reflected from it and that of a relatively narrow range in wave length. To see the possibilities in this field one has but to make visual examination of various natural and artificial colored objects through various photographic filters. Photography in natural colors is made possible by a number of processes but it will not be considered in the present paper for two reasons; first, because the writer has had no personal experience with these processes and second, because it appears unlikely that it will be used to any considerable extent by geologists in their professional work in the near future.

The materials to be used will have been in part determined by the choice of a camera. If this was of the roll film type there is relatively little choice to be made in the matter of films. In many, one might say most, cases it is desirable for the geologist to secure a goodly supply of film before going to the field and in such instances this is best packed in foil or other airtight "tropical" container.

If a plate camera is used and many photographs are to be taken incidental to long daily trips the film pack will be desirable since the weight is slight in comparison to that of either plates or films in separate holders. If not over six or eight exposures are made in a day separate holders containing cut film can well be carried. In this case some may be of ordinary portrait or commercial grade and a few orthochromatic or panchromatic. Orthochromatic film is being increasingly used for general purpose work as well as for special subjects and the writer feels that it might profitably be substituted for most routine field work with plate cameras. The same is, of course, true of plates with similar emulsion but it is unlikely that many geologists will prefer the plates to the lighter cut films. Panchromatic films aside from being slightly slower than other grades are equally useful on all subjects and are essential if the deeper filters such as red, orange and green are to be used.

TRIPODS AND SUPPORTS

Some sort of tripod is essential as is urged by the writer at great length elsewhere. On the score of weight the tripod is always something of a burden and there seems to be little escape from this difficulty. Many different sorts of tripods have been devised in America and abroad with object of securing the greatest rigidity

with the least weight. From this standpoint the folding wooden tripod is probably the best but it is less convenient and more bulky than the tubular telescopic metal tripods. The latter deteriorate in stiffness more rapidly than the wooden tripods in the course of the necessarily rather rough usage attending field work but appear to be about as good as any available for the lighter cameras. For the larger view cameras wooden tripods of ample size are very satisfactory.

A number of types of clamps and universal joints are obtainable for the smaller cameras. Of these the writer has found the form designated as the Optipod by the Eastman Kodak Company to be very convenient both as a universal joint for use with the tripod and also as a substitute for the latter in connection with some other support. By modifying the shape of the jaws to a slight extent this instrument can be made to take a tighter grip on objects not injured by marring and has been used extensively by the writer in conjunction with his geologic hammer. The latter can be driven into a slight rise on the ground, or into a fence post or tree and the optipod then attached to the handle. Another method is to build a rude tripod or lean-to pile of any available sticks and clamp to some part of this. By such methods the writer has found that in some types of country it was possible to get on without carrying the tripod and still to support the camera for time exposures for nearly all pictures. Some sort of universal joint is worth its weight in places where it is difficult to find footing for the tripod and at the same time direct the camera with accuracy toward the desired subject. With the joint one can use the available footing even though it be very unsymmetrical and then do the aiming as another operation with the adjustment afforded by the ball and socket. If many detailed pictures of small objects lying on the ground or in out of the way places are to be attempted the universal joint is indispensable since by its use the camera may be pointed directly down or in any other direction with equal ease.

The writer has not seen an equally satisfactory universal joint for larger cameras on the market but has used a simple one of his own construction for a number of years. This consists of a simple right angle of $\frac{1}{4}'' \times 1\frac{1}{4}''$ band iron with arms of 2'' and 6'' respectively. Each arm has toward the end both a clear $\frac{1}{4}''$ hole and a hole tapped with $\frac{1}{4}''$ -20 thread (approximately the standard socket thread). With the angle is an extra tripod screw which is kept in

one of the tapped holes when not in use. The angle is clamped at the top of the wooden tripod by means of the tapped hole in either arm and the camera then clamped sideways to the other arm by means of the extra screw and clear hole. The angle is thus rotatable on the tripod and with the motion of the camera on the other arm provides for it a full alti-azimuth mounting which is far more rigid than would be a clamp with movable parts. The device weighs nearly a pound but is still proportionately light compared to the camera it supports.

Some tripods may be fitted with tilting heads which serve the same purpose as universal heads. As in the case of tripods themselves these are difficult to construct of the requisite strength combined with lightness and are worth examining with care or trial in actual use before purchasing.

Stereo photography is becoming more popular among amateur photographers and is of great value to geologists in certain instances. It is doubtful if stereo cameras with their necessary extra bulk will be carried for routine work but occasional stereo pictures may be taken by moving the camera between two successive exposures. A light, flat metal link of a length half the desired shift has been used by the writer and makes the shift more easily achieved than if the whole tripod were to be moved. Dr. F. E. Wright¹ suggests a shift of from one to five percent of the distance to the principal object to be photographed.

EXPOSURE METERS, TABLES AND COMPUTING DEVICES

There are many mechanical devices for determining the exposure to be given under any set of conditions. There are many very successful photographers who estimate exposure as the result of experience without reference to any sort of artificial aid. The writer has used a few of the devices which are available and has also done considerable satisfactory photography without any of them. He feels that the best procedure for the average person is to use some one of the many good calculating devices and at the same time for each picture estimate previously to using the calculator the exposure he would give. He can then compromise between his own estimate and the reading of the calculator and let the finished picture be the proof. On the one hand the constant effort on the part of the operator to forecast the result of the calcu-

¹ Wright, F. E. Private communication.

lation, which may be considered in most cases reasonably correct, and on the other hand his observation of just how his estimates differ justifiably from the calculated ones prove to be very effective in building up a vivid exposure instinct or judgment.

The various exposure determining devices may be divided into four classes. The first class consists of meters proper or actinometers which make a direct measurement of the light at the time the picture is taken by means of sensitized paper. These are useful in connection with landscape or architectural photography but are less satisfactory in detail photography where one is concerned with the light reflected by a small object. The second class includes the type of meter in which the light is judged by viewing through a wedge or series of screens of variable density. These have the advantage that one can deal with the light directly and exclusively from the subject. They are subject however to the disadvantage that the human eye varies greatly in its susceptibility to light under varying conditions. Even with the precaution of allowing the eye to come to rest by closing it for a time there is doubtless much variation in the readings obtained from identical lightings of the same subject with variations in the condition of the eye of the observer. In spite of this drawback this type of meter is probably among the most useful. The third type consists of the numerous calculators, circular and linear. These are all similar in that they take account of condition of the sun, time of day, season of year, nature of the subject, speed of the film and aperture of the lens. They also employ in common the logarithmic slide rule principle in the computing. They differ in the arrangement of the various factors and movable parts and in the range and manner of statement of the various factors. They are the most convenient and portable of the four types and illustrate most vividly the effect of the various factors in controlling the tremendous range in practical exposure times under various conditions. The fourth type is the exposure table such as that issued by American Photography. These tables are more complete than any of the calculators and handle a wider range of conditions. They consist essentially of a series of logarithms (to the base 2 or 4) of the values of the several factors which may conveniently be added mentally to secure the logarithm of the exposure.

MISCELLANEOUS ACCESSORIES

For work with the larger view cameras a focusing cloth will be needed. Rubber backed bellows cloth is more completely opaque but plain black cloth is less warm to work under and will do for most conditions. With some ground glass cameras a small collapsible hood is attached and in these a sufficient view of the image is available without the focusing cloth.

A changing bag permits loading and unloading of films in the daytime and will be needed where many pictures are to be taken in one day on cut films or plates. At night away from bright artificial light one may find many places where plates, even of panchromatic grades, may be changed safely, if one works quickly and with due care.

A self timer is useful in some instances. For example if one wishes in the picture to point to a certain contact and is working alone he may by means of the self timer be able to appear in the picture. In other cases where brush has to be held aside the self timer may be used to advantage.

The choice of ray-filters will depend on the films which are to be used. If one or two only are carried those in slip-on mounts are most convenient. For using a larger number interchangeably the writer has a small cell which slips on the lens cell and holds in turn the filter by means of a light spring ring. The filters used are unmounted but cemented in glass. He has carried six of these filters in chamois pockets in a metal pill box daily for nearly twelve months in the tropics without breakage and without serious deterioration.

For most subjects a yellow filter (K₂ of Eastman Co.) is best, next to this the orange (G), red (A), deep red (F), and green (B) are useful in the order named. All of the last named can be used only with panchromatic films or plates. Exposure factors and other data for the use of these filters can be obtained from the makers.

Lenses should be kept clean, preferably by good protection rather than by wiping. A small and thin lens cap is useful for this purpose especially in the tropics and in damp situations. If absolutely necessary to wipe a lens, the dust should first be dislodged by holding the lens inverted, and brushing or flicking the dust from the surface as it may contain hard particles which would scratch

the glass. A clean piece of soft cloth may be used to wipe the surface gently but tissue paper or special lens paper is best of all and if protected will always be clean.

Methods of carrying the camera and accessories will differ according to personal choice. To some a carrying bag seems most convenient and others prefer a sling case or some sort of belt attachment. The writer cannot refrain from urging the adoption of some systematic plan for the transportation of the camera and other photographic equipment and the provision of small cloth or leather bags or cases to exclude dust and afford reasonable protection to the instruments. At best field work is hard on instruments of all sorts but the condition of some cameras, compasses, barometers and handlevels the writer has seen in the hands of geologists was due to lack of even ordinary care and attention in the matter of drying and cleaning. Several of the instruments mentioned above cost as much and are worthy of the same care as a good watch.

FIELD PRACTICE

PRE-FIELD TESTING

Unless one takes into the field only equipment of which he has made frequent and recent use it is desirable to make a few tests to make sure that it is in working order and to become accustomed to any peculiarities it may possess. There are a number of defects not readily noticed which might easily cause the entire loss of many pictures if not detected. Leaks which admit light may occur in the bellows or in other parts of the camera or the slides or backs of plate holders and film pack adapters may be similarly defective. Lenses sometimes become loosened or uncemented and cause poor definition or flare. The focusing scale may not be properly placed or may not be accurately graduated. The upright yoke which carries the lens not uncommonly becomes bent and changes the focus relation, especially in cameras with short bellows. The focus may readily be tested on a roll film camera by removing the back and laying a ground glass strip with its ground side in contact with the rollers. If the ground glass is not convenient a strip of tracing cloth or paper stretched taut may be used.

One of the features most in need of testing is the shutter. This should work decisively and if not with times as marked the actual

times should be known. There are various methods of testing the speed of shutters of which a few will be mentioned. A bicycle wheel carrying a single bright object on its outer edge can easily be rotated at a speed which is known within 5 percent or less. This should be photographed from a point near the extended axis of the wheel using the several speeds to be tested. The aperture and lighting should be such as to give a fairly strong image for the bright spot. After developing the film or plate the amount of angular motion can easily be measured and the speed computed. With a little planning all the speeds marked can be tested on one or two films if the general lighting is dull enough so that most of the view is much underexposed and the camera is pointed differently for successive views. Any piece of machinery rotating at known speed and carrying a bright spot (such as a thumb tack illuminated from behind with a strong light) can be similarly used if the speed be of about the right value. From one-fourth to a full revolution during the exposure is best for accurate measurement.

A very simple method is to arrange two carbons to give a small arc light on an alternating current circuit. If this light be photographed in a dark room while swinging the camera about slowly the image will be a line of dots. In the case of a 60 cycle circuit there will be 120 flashes per second and exposures from $1/50$ up to two or three seconds can be measured with reasonable accuracy.

A falling body or a pendulum may be used but the computation would be somewhat more difficult than in the foregoing examples. Various other methods will occur to anyone needing to test a shutter, according to the facilities he has at hand. The writer has never attempted it but a satisfactory test could probably be made by photographing at short range an automobile traveling at known speed.

PLACING THE CAMERA

In placing the camera the first and prime consideration is visibility of the feature it is desired to portray. In open country this matter offers little difficulty but in a wooded region the vegetation sometimes interferes either with getting a view out from the camera stand to a distant object or with getting a view in toward a shaded rock feature. Another factor which has to be considered

at the same time is the support for the camera. If the picture is to be taken as a snapshot this part is easy but for a time exposure one has to have suitable footing for the tripod or some object to which to clamp the camera. If a tree or other solid object is at hand the camera may be blocked upon it or held against it with or without blocking in almost any position. Such a position may prove a little awkward for focusing on the ground glass but in most cases this may be done "free-hand" and such slight errors as are present in the focus are more than taken care of with the increased depth resulting from using a small stop. If one uses a tripod a universal joint will be found extremely convenient in orienting the camera in difficult situations after some sort of footing for the tripod has been found.

A third factor which should be taken into account so far as possible under the limitations imposed by those of visibility and support is that of most favorable viewpoint and lighting. Features which can be conveniently visited at any time of the day enroute to more distant places or which are of sufficient importance should be studied in order to choose the most effective light conditions. Practically all the features which geologists have occasion to photograph will be found to be more clearly outlined in the oblique rays of the mid-morning or mid-afternoon sun than in that of noonday and with a reasonable amount of intelligent practice in estimating exposure good pictures may be taken from sunrise to sunset. Low terraces and similar features are frequently uniformly grass covered and hardly distinguishable except in early morning or late afternoon light. In the case of detail views of rock surfaces the choice of time depends on the attitude of the surface in relation to the sun. Such subjects as glacial striæ or slicken-sides which depend on very sharp oblique light for their proper illumination are not always situated in such a position that the sun ever strikes them properly. (Figure 1). These may sometimes advantageously be illuminated with an artificial light at night or by means of a mirror after shading them from the direct natural light.

In photographing objects directly toward the sun, which is sometimes necessary or even desirable, care must be taken to shade the lens, especially if a wide aperture is used. Many subjects will appear best when entirely in the shade. This is particularly true of such features as bedding, schistosity or other struc-

tures in which the chief distinction between different parts is a color difference rather than a difference in relief or configuration. If such a surface has any considerable irregularity and is photographed in bright sunlight there is danger that the essential color differences will be entirely subordinated to the incidental light and shade distinctions.

In addition to the problems of placing the camera under normal conditions there are those of keeping it placed in a high wind or keeping it dry in rainy weather. If camera or holders become wet superficially they should be wiped at the first opportunity and laid where they can become thoroughly dry. Salt water and spray are particularly insidious because the deliquescent salts maintain a condition of stickiness and are rust breeders in addition to the damage to films. Camera and film cases of rubber coated cloth are very useful in wet regions.

FOCUSING

Objects 100 feet or more away offer no problem in focusing but for nearer objects the camera must either be focused on a ground glass or by means of a scale set to the estimated distance. If the view involves a considerable range of distances for near objects one should focus or set to some feature which is about midway on the focal scale of the whole field of view and use a very small stop. If it is desired to include distant objects and foreground in the picture the focus should be set midway (on the focus scale) of the two distances and the lens stopped down to the necessary small aperture. (Figures 2 and 3. See table of depths of definition).

It is desirable in many detail pictures to place some object of known size in the field of view to serve as a scale. In such a case the object, such as the geologist's hammer, his pencil or some other convenient object should be placed as unobtrusively as possible toward the bottom or one side and objects of unusual character or of temporary interest avoided as much as possible. In views of large rock exposures a human figure makes a good scale but should not be so placed as to divert interest from the geologic features. (Figure 4).

CHOICE OF PLATES OR FILMS

If one is operating a roll film camera the choice may be con-

sidered to have already been made. With a plate camera there are a number of grades of film or plate which may be used according to the nature of the subject. Probably the best for standard use is some good make of orthochromatic cut film. For a few subjects such as rock exposures which are wholly in sunlight or similar objects with little color variation there is little purpose in using a color filter but most pictures will be considerably improved by the use of a medium filter such as K2. Clouds will be made more distinct and visibility through nearby haze increased by such a filter. Views which unavoidably combine brilliant sunlight and rather deep shadows can usually be taken more successfully with a filter than without. Very distant haze-obscured skylines require a deeper filter such as the red F and a panchromatic film for their successful delineation. (Figures 5 and 6). The lighter red A and the orange G are occasionally useful in taking geologic subjects and more rarely the green B filter. (Figure 7).

For the photography of bright colored objects, such as flowers, animals or other natural objects filters and orthochromatic or in some cases panchromatic films are essential. It is rarely that the geologist will have occasion to seek exceptional rapidity in the films he uses and it is well to remember that the medium speeds of film have greater latitude and finer grain than the faster ones. In a very few instances the use of process films with their very great contrast is desirable but it should not be undertaken unless other methods have failed to secure pictures of very flat subjects and one can check upon the films by having them developed at once. The latitude of these films is so slight that the exposure must be estimated with much greater care and the contrast is so great that objects with any range of light and shade are likely to produce disappointing results.

DETERMINATION OF EXPOSURE

The factors involved in determining the length of exposure for a given picture are as follows:

1. Latitude
2. Season of year
3. Time of day
4. Condition of sky and atmosphere
5. Distance of object
6. Illumination of object

7. Color and lustre of object
8. Speed of film
9. Filter
10. Aperture of lens

Fortunately the calculation of exposures from these ten factors does not need to be carried out with great numerical accuracy. In fact in practice several of the factors can be ignored most of the time if the operator is alive to the relative importance of all the factors and knows when a given factor becomes of large importance. For operations from day to day, the latitude and season of the year are constant and need be taken into account but once. The speed of the film is another factor which need be considered only as one changes to another grade. Other factors may be combined in making rough mental calculations. For example the distance, illumination and color of objects may all be combined under the general head of subject. For a number of years the writer has used a scheme for simplifying the calculation of exposure which has proved to be very useful. It is based on the principle that the exposure time and the area of the aperture are inversely proportional for a given set of conditions. In other words for a given subject and lighting a definite amount of light must be admitted and it is immaterial from the standpoint of exposure whether this be accomplished quickly through a large aperture or more slowly through a correspondingly smaller aperture. In computing exposure we can therefore concern ourselves first with the amount of light to be admitted as the main problem and then solve at our convenience the subordinate problem of the aperture and dependent time of exposure with reference to the needed depth of focus, stopping of motion or other considerations. The practical application of this method consists in the establishment of a series of numbers which are proportional to the net brilliancy or photographic powers of a series of subjects and which are obtained by dividing the appropriate U.S. stop number by the proper exposure time in seconds. By temporarily eliminating factors one, two, eight, nine and ten from consideration and combining the other factors it is possible for one gradually to build up in memory the results of accumulated experience in some such fashion as shown by the table below. The values given are those indicated roughly by the writer's experience; each worker will do best with a scale of his own making.

CONDITIONS	BRILLIANCY NUMBER	STOP-TIME COMBINATIONS
Bright sun Average landscape	200	U.S. 4 - 1/50 U.S. 8 - 1/25 U.S. 40 - 1/5 etc.
Bright sun Distant marine view, clouds	800	U.S. 16 - 1/50 etc.
Bright sun Near view of quarry face, 50 feet	50	U.S. 4 - 1/12 about U.S. 128 - 2 1/2 about
Dull light Shade, near view of outcrop, 10 feet	5	etc.

It will be apparent that it is vastly easier to remember a series of numbers such as 200, 50, 25, 10, etc., than to keep in mind the numerous combinations of stop and time which have been used in various equivalent situations. In the use of this system the results obtained in the fundamental scale can easily be modified for effects of latitude, film speed and filter according to theory or the operator's experience.

The use of exposure computers or meters along with such a mnemonic system will enable one to build up a memory scale more rapidly, to observe more closely the various values of the different factors and suggest modifications to the results given by the various devices under special conditions and interpretations peculiar to the operator. More complete data are contained in the American Photography Exposure tables which are of great value for occasional reference even if not used for every exposure.

At the outset it is very desirable to have an idea of the total arithmetical range represented by the various factors which affect

exposure and the writer has attempted to indicate some of these in the table below. (Figure 9). The numbers given may be

TABLE SHOWING RANGE OF NOON ILLUMINATION FOR LATITUDE		
Latitude	Relative Brilliancy	
	Summer	Winter
0 - 20	1	3/4
30	1	3/8
40	1/2	1/4
50	1/2	1/10
60	1/2	1/12

TABLE SHOWING RANGE OF BRIGHT SUN ILLUMINATION FOR TIME OF DAY LATITUDE 40°		
Hour	Relative Brilliancy	
	Summer	Winter
12	1	1/2
11 1	1	1/2
10 2	1	3/8
9 3	3/4	1/4
8 4	1/2	1/16
7 5	1/2	1/32
6 6	1/4	
5 7	1/32	

advantageously used to modify the brilliancy numbers in expanding the table given above.

Filters vary in their required exposures from 2 to 30 times the normal according to the color and density. If we take the range of basic subject exposures as from 1 to 2000, that of the season and latitude factors as 1 to 12, of the time of day 1 to 32, of the filters 1 to 15, and of film speeds it will be apparent that the range in exposure required is very close to 1 to 12,000,000. If to this enormous range we add the effect of variation of apertures we find the possible theoretical range in exposure times is of the order of a billion fold.

When the amount of exposure needed has been estimated there remains the single problem of choosing a stop and thus determining the time of exposure. There are several possible governing considerations. If the exposure is to be made while holding the camera in the hand the exposure cannot safely be made longer than 1/25 second by most people. A few can, by standing very rigidly and holding the breath, make exposures of 1/10 second or more without blurring the picture but this should not be attempted until the operator has made a number of tests near to the laboratory to learn his individual limitations. The speed of moving objects, such as that of a breaking wave or of a tree swaying in the wind may determine the greatest permissible exposure time. If considerable depth of focus is needed for details of close objects or to bring a foreground in sharp focus it will be necessary to stop down to a small aperture. (Figure 2). The depth of focus obtained for different apertures and focal lengths is given in the table below. So many possible errors, some inherent in lenses and others inherent in the adjustments and nature of the subject, are eliminated or reduced by using time exposures and small apertures that the writer in common with many other geologists has found it advantageous to follow this practice with a large proportion of the pictures taken, including landscapes. To those who take great pride in the performance of a high grade anastigmat lens such advice may seem not to leave room for individual skill and craftsmanship but it is the writer's belief that other aspects of photographic technique offer abundant opportunities for exercise of skill and that in the tremendously practical and necessarily secondary business of taking geologic photographs the chance of correcting many difficulties in one operation should not be ignored.

Among these are faulty estimates of distance, poor adjustments of camera parts, lenses inferior to the best, and depth in the subject. (Figure 8).

MAKING THE RECORD

A record should be made at the time the picture is taken. This should include the approximate date, the location of the subject by state, by section or project and specifically on a map like any other geologic observation. A full title and statement of the import of the picture should be recorded. The photographic data such as time of exposure, aperture, time of day, conditions of lighting, etc. are not needed for the geologic record but are invaluable to one who is attempting to improve his percentage of good pictures. By inspecting and criticising the negatives when they are returned from the laboratory with the record of conditions in hand one's technique is improved more rapidly than by any method except that of developing the pictures immediately after they are taken.

Film should be developed as soon after exposure as possible since films deteriorate much more quickly after exposure than before. Under favorable climatic conditions films may be kept for several weeks without marked change but the practice is not good where other arrangements can be made, not only because of chance of spoiling but because of the desirability of knowing the quality of results while still in the field.

TABLES

Many useful tables are contained in booklets of the Eastman and other camera makers and in photographic magazines. The following are presented as those most frequently used in the field.

TABLE OF HYPERFOCAL DISTANCES ¹					
Focal Length	f/4.5	f/8	f/16	f/32	f/64
8"	250	141	70.4	35.2	17.6
6"	142	80	40	20	10.0
5"	99.5	56	28	14	7.0
4"	64	36	18	9	4.5
3"	37.5	21.1	10.6	5.3	2.6
2"	17.2	9.7	4.8	2.4	1.2

¹ The hyperfocal distance for a given aperture and focal length is that

DEPTH OF DEFINITION TABLE

Lenses commonly used on size	Distance focused on	f/4.5	f/16	f/64
3¼" x 5½"	100	60'-inf.	32'-inf.	10'-inf.
	25	22'-28'	17'-52'	8'-inf.
	6	5 ⁹ / ₁₀ '-6 ¹ / ₁₀ '	5½'-6¾'	4½'-10'
3¼" x 4¼"	100	48'-inf.	21'-inf.	7½'-inf.
	25	20'-33'	13½'-inf.	6'-inf.
	6	5¾'-6 ¹ / ₃ '	5'-7½'	3¾'-20'
2¼" x 4¼"	100	35'-inf.	17'-inf.	6'-inf.
	25	18'-30'	11½'-inf.	5'-inf.
	6	5 ² / ₈ '-6½'	4¾'-8¼'	3½'-inf.

beyond which all objects are in focus when the lens is focused at infinity. This table is computed on the basis of a circle of diffusion of 1/200 inch. Below the heavy line are allowable aperture — focal length combinations for sharp foreground with a camera levelled on level ground.

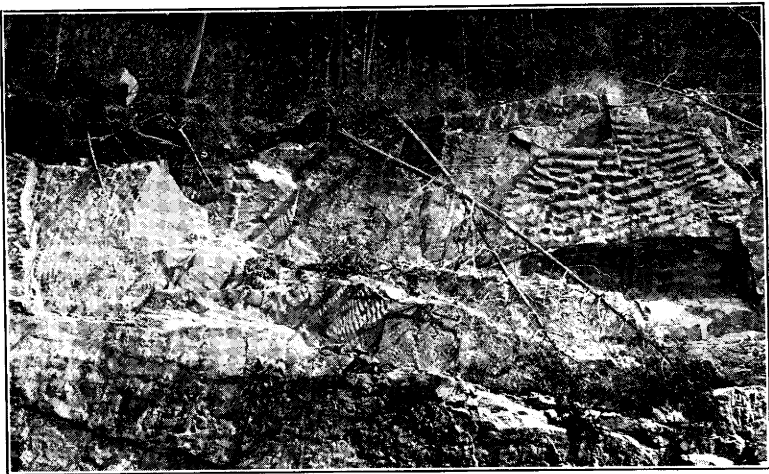


Fig. 1. Ripple marks on several bedding planes in Proterozoic quartzite. Baraboo Region, Wisconsin. An example of a photograph to be taken successfully with the sun in one limited position at a definite time of day.

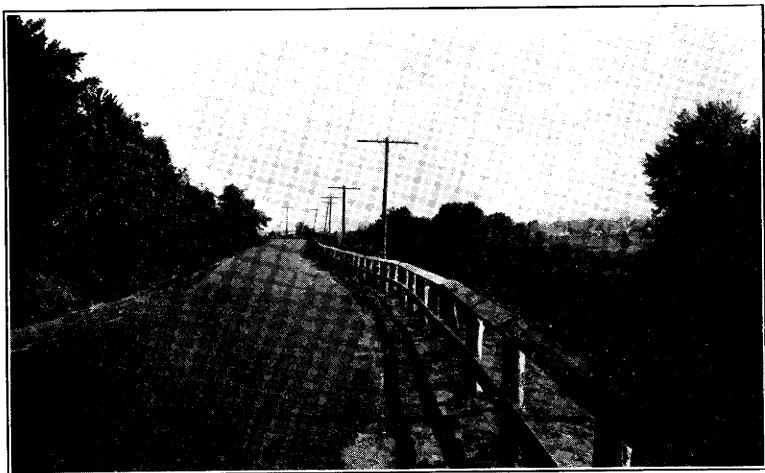


Fig. 2. View near Washington, D.C. Showing result of using small aperture to give depth of definition.



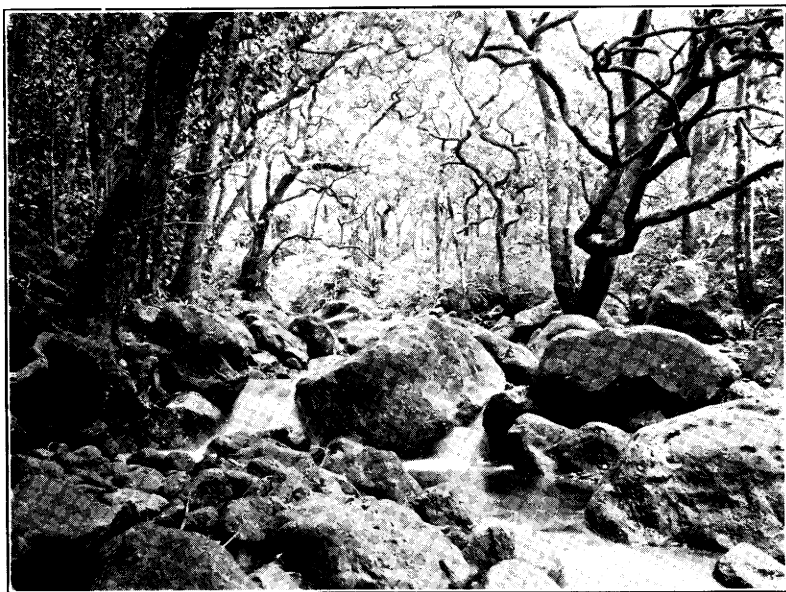


Fig. 3. View of channel of Mapulehu Stream, interior of East Molokai, Hawaii. A view requiring a small aperture for depth of definition even at the expense of sharpness in the moving water.



Fig. 4. Outcrop of Pennsylvanian coal measures near Dante, Virginia. An example of the unobtrusive use of the human figure as a scale.



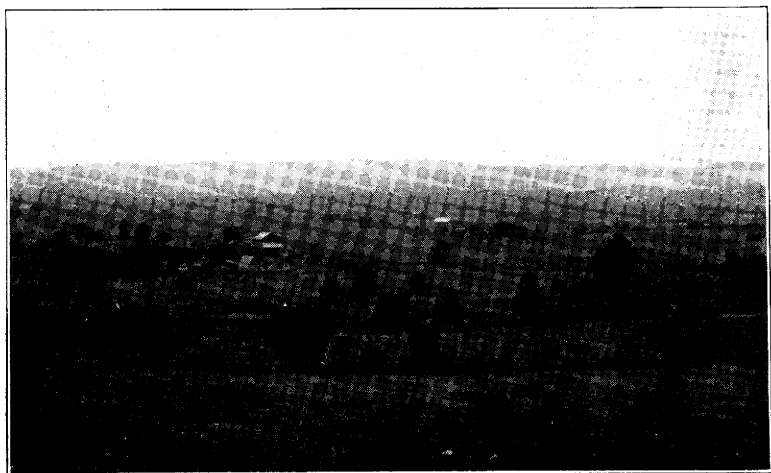


Fig. 5. View across Monocacy Valley in Maryland. Taken with portrait film and no filter. Detail is missing in the distant portions of the view. See Fig. 6.

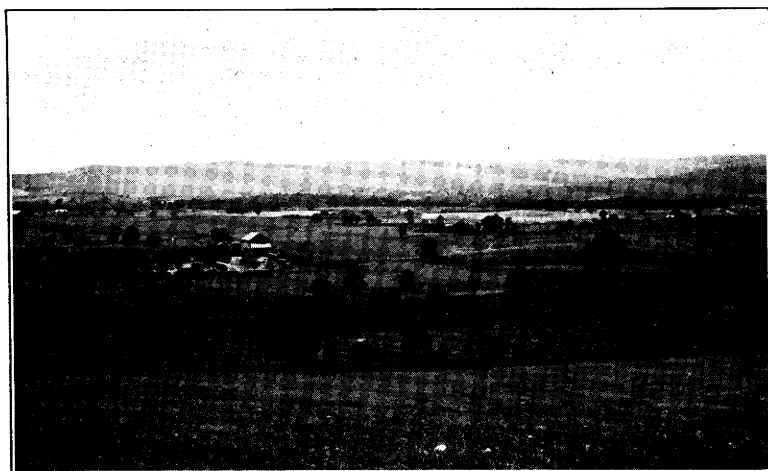


Fig. 6. Same view as Fig. 5. Taken with panchromatic film and deep red filter (F). The improvement in detail in the middle and distant parts of the view is apparent.

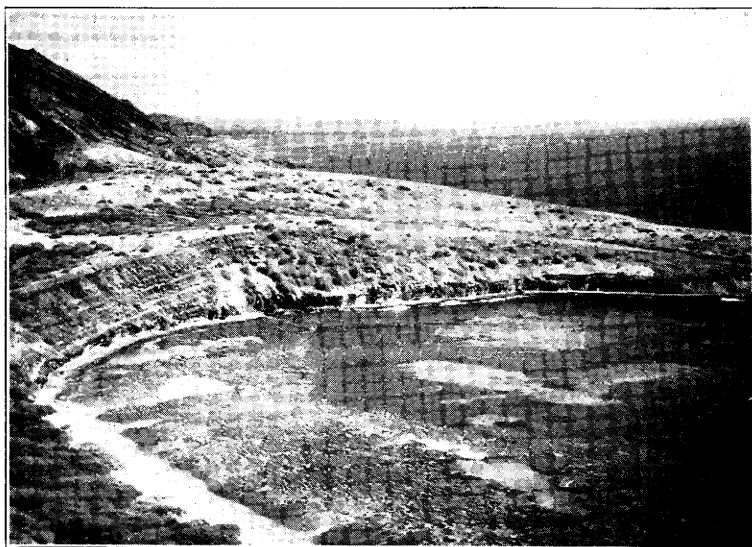


Fig. 7. View of Hanauma Bay, Koko Head region, Oahu, Hawaii. Taken with panchromatic film and orange (G) filter. The delineation of underwater reef detail over the entire area of the bay would be far less satisfactory without the filter and appropriate film.



Fig. 8. Detail of weathering of shale, near Norton, Virginia. Taken with auxiliary lens of portrait type. Example of satisfactory definition wrought over oblique field with a very imperfect optical system by means of very small aperture.



Fig. 9. View of fall in glen at Pictured Rocks, northeast Iowa. Taken at about 7:30 P.M. in late April in dark, shaded glen under trees. Exposure about ten minutes with $f/32$ aperture. Showing large increase in necessary exposure at late afternoon hours and satisfactory results if this condition is met.



THE DESERT STRIP OF WEST MOLOKAI¹

CHESTER K. WENTWORTH
University of Iowa

INTRODUCTION

LOCATION

The west end of the island of Molokai is crossed by a strip of barren windswept country in which eolian features are developed with exceptional clarity and vigor. From a point on the north coast about seven miles east of the northwest cape this desert area extends in a southwesterly direction nearly to the west coast and has a length of about five miles and a width of about a half mile. Its location as well as other salient features of the island are shown in Figure 1.

GENERAL DESCRIPTION

The desert strip is due to persistent drifting of calcareous sand over the northwest upland by strong northeast trade winds. The sand is derived from two or three miles of sea beach at Moomomi on the north coast. Landward of this beach is a dune belt a half mile or more in width. The sand from the eastern end of this strip is not blown far inland but that from the western end is carried up a slope which averages about 10 percent or nearly 6 degrees to an elevation of over 600 feet and thence over the gradually declining upland for nearly three miles farther. (Figure 2). The writer visited the region at a time when the trade winds though persistent were of moderate strength and were moving a relatively small amount of sand. The testimony of observers who have crossed the strip during periods of strong wind emphasizes its activity as a transporting agent and the painfulness of attempting to face the flying particles of sand.

There is a nearly continuous cover of calcareous sand on that part of the strip which lies nearest the beach source and extending up well toward the highest part. Continuing in the direction of the wind the sand becomes less abundant and is confined to small

¹ Published by permission of the director of Bishop Museum.

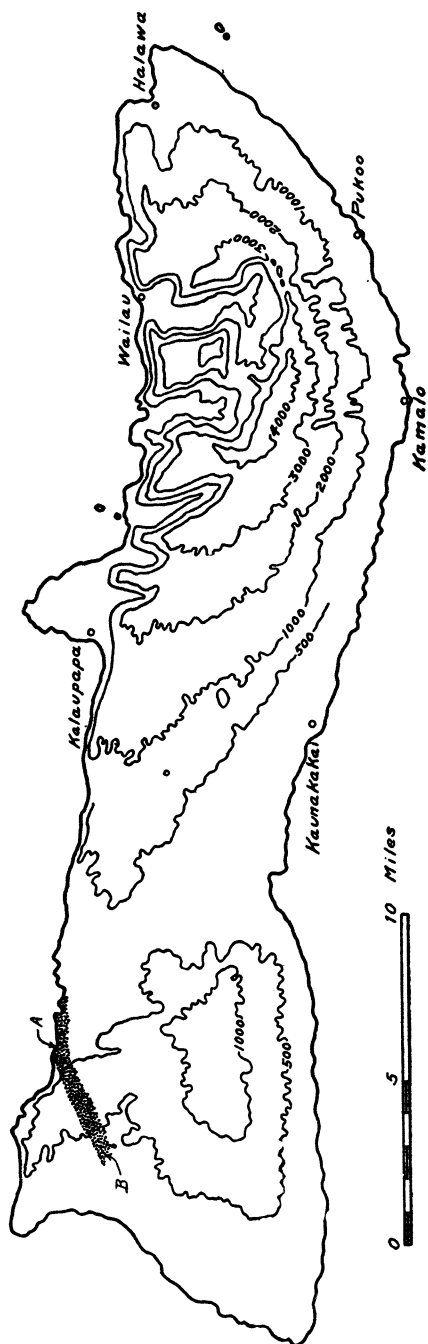


Fig. 1. Contour map of Molokai showing desert strip (stippled) on the west end. Topography shown by 500 foot contours on west end and by 1000 foot contours on east end, except that the 500 foot line is shown in the gap between east and west Molokai. Data from preliminary map, U. S. Geol. Survey.

dunes and linear ridges and to very subordinate quantities which lodge against and around occasional obstructions. At the southwest end of the strip there are extensive deposits of sand filling the heads of some of the smaller gulches and banked over the windward wall of Kakaako Gulch. At present this deep gulch constitutes an obstacle which the sand does not pass in appreciable amounts and no evidence was seen by the writer that it has been extensively blown to the far side at any time in the past.

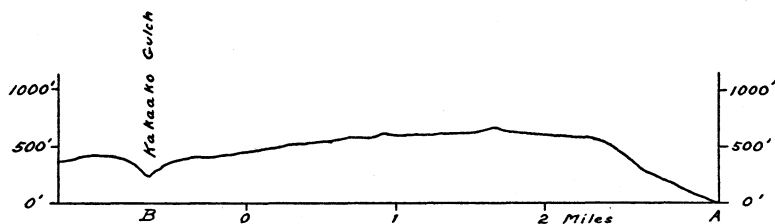


Fig. 2. Longitudinal section of the desert strip. Vertical scale exaggerated four times. See Fig. 1 for location.

Downstream from the end of the desert strip Kakaako Gulch is notable for the amount of fine sand which is incorporated in its alluvium and large quantities of the sand no doubt reach the sea at the mouth of this gulch. At the leeward end of the strip the sand is buff to brown in color and contains many grains of weathered basalt from the upland in addition to the fundamental organic constituents, but on the steep slope at the windward end the sand is whiter and more largely consists of debris from corals, algæ, molluscan shells and foraminifera.

In those parts of the desert which are not wholly covered with sand the surface is commonly abraded to a level from one to five or rarely ten feet below the original soil layer which is preserved in a few small boat-shaped remnants which are capped with sand mounds and rise to eight or ten feet above the eroded surface. Immediately below the old soil level the basaltic geest is deep red in color but becomes increasingly lighter colored with depth and at eight or ten feet is commonly a mottled yellow or orange and gray. Apparently wind abrasion becomes increasingly slow as it reaches the more resistant gray geest and it has at no place uncovered sound basalt in place. In a few places near the west end of the desert the surface consists largely of gray basaltic spheroids which have been uncovered by the wind and a few of these are isolated at other points.

CLIMATE AND VEGETATION

The climate of Hawaii as a whole is characterized by low annual and daily temperature ranges, by the persistence of trade winds from the northeast and by the dependence of variations of rainfall on the local geographic factors of elevation and exposure to the prevailing winds. For the most part the southwestern and lower parts of the various islands are dry whereas the higher parts and especially those with northeast exposure have heavy rainfall.

No climatological data are available for the section of Molokai in which the desert strip is located but certain general estimates can be made. The northeast part of the desert is exposed to trade winds blowing from over the ocean and rises fairly steeply to more than six hundred feet. It is probable from what is known of rainfall at stations on the higher, eastern part of Molokai that the rainfall on the eastern end of the strip may be as great as 20 inches. The western end, which is lower and farther from the sea receives less rainfall, perhaps less than 10 inches.

The average hourly wind velocity is probably about 10 miles an hour. At times the velocity is very much greater than this, probably occasionally reaching 40 or 50 miles an hour. It is probably very rarely that the wind departs from the northeasterly direction indicated by the linear, parallel-sided form of the desert strip. Monthly mean temperatures of other localities on Molokai not far from the desert range from 68 in winter to 79 in summer and the mean annual temperature for the desert is believed to be about 72 degrees.

Practically no vegetation grows on the bare surface of the basaltic geest. Such plants as are present in the desert are those which grow on the overlying dunes and sand patches. None of these plants were collected but a few have been tentatively identified from sketches in the writer's notebook by Dr. Forest Brown of the Bishop Museum. These, the most abundant elements of a somewhat limited flora, were as follows:

Scaevola lobelia
Lepturus repens
Ipomœa pes-capræ
Heliotropium curassavicum
Boerhaavia tetrandra
Xanthium strumarium

No material was obtained which permitted the identification of

the shrubs imperfectly preserved in the form of calcareous casts of roots and stems in some parts of the desert strip.

ACKNOWLEDGEMENTS

The writer is indebted to Mr. Fred Ohrt, to officers of Libby, McNeill and Libby, and to Mr. and Mrs. George Cooke for much assistance and many courtesies extended to him in the course of his studies of west and central Molokai. Without the hospitality with which he was met on all parts of Molokai it would have been impossible for him to have covered a considerable part of the island in the time available.

DESCRIPTION OF EOLIAN FEATURES

LARGER FEATURES OF THE DESERT

Sand Formations. Three formations are to be distinguished by their physical condition. The oldest of these is a compactly cemented eolian sandstone which is found at a number of places along the margins of the present desert strip on both sides and extending the width of the eolian formations to at least a mile. This sandstone is buff colored on fresh surfaces and gray white on the weathered surfaces. It shows typical eolian bedding with curved planes mostly tangent below and truncated above. The surface of the formation is deeply weathered into pits and channels forming a deep cusped profile with the sharp points and ridges pointing upward. This sandstone is considerably more abundant on the north side of the strip and forms together with some marine sandstones a great headland just west of the sandy beach on the coast.

The next younger formation is yellow to buff dune sand which is slightly cemented in places but is hardly to be called sandstone. This, likewise, is of typical eolian structure and lies in long oval mounds in close association with the modern sand dunes. These and the modern uncemented sand which is drifted and lodged here and there on the desert area constitute the third formation.

Dunes and Remnantal Sand Mounds. The commonest form of sand accumulation is that of an elongate mound of which the windward slope is somewhat less steep than that of the leeward side. The mounds are of all sizes from a few yards in length and ten feet high to several hundred yards long and 50 feet high. No

well-marked crescentic dunes were seen. After accumulation has ceased the mounds, together with the underlying pedestal of geest, are subject to erosion and the windward slope then becomes steepest, the side slopes slightly less steep and the leeward slope most gentle of all. The relations of these sand mounds to the underlying surface are shown in Figure 3.

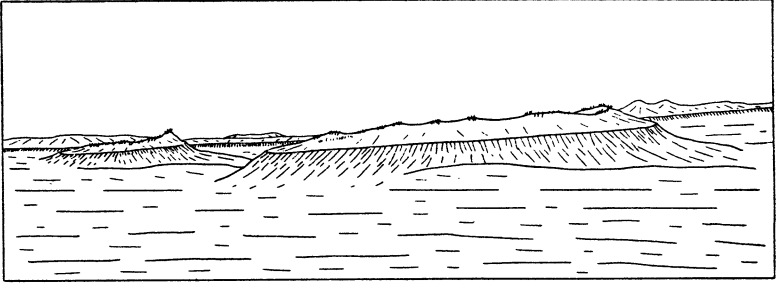


Fig. 3. Sketch showing erosion remnants of geest surmounted by sand mounds. Note the distinct line of the old surface between the two. View looking northwest, wind moves from right to left.

Leeward Crowding of Channels. At several points where the sand from the desert strip is drifting into gulches and small channels the windward side of the channels is almost completely covered with sand lying at the angle of rest of about 30 to 31 degrees. The leeward side, on the contrary, shows bare basalt walls and evidence that the ephemeral streams which flow in it are forced to the leeward side by the continuous infall of sand on the other side. There can be little doubt that over a period of many years this process results in a considerable shifting of the channel since the windward wall is largely protected both from abrasion and from surface weathering, while the leeward wall which faces to windward is subject both to stream and wind abrasion.

Dune Structures. The two most prominent types of structures in both the modern sand and the older eolian sandstones are talus bedding in which the beds dip at the angle of rest of about 31 degrees and what may be called whaleback structure. The latter consists of curving beds which lie parallel to the surfaces of the elongate oval mounds, being nearly horizontal at the crest and dipping increasingly outward toward the sides and similarly but less markedly toward the ends. This type of structure is seen

in many of the old masses of eolian sandstone and constitutes conclusive proof of eolian origin.

Desert Profiles. In looking transversely across the desert strip from either side one is impressed with the strong vector character of the profiles. This is especially true if the horizon itself is a part of the desert surface. The windward slopes of the elevations are steep or even eaten back so as to be overhanging. The leeward slopes are much more gentle and in general continue at a uniform angle down to the general level. It is to be noted that this relationship between steeper and gentler slopes is the reverse of that shown by most sand dunes in which the leeward slope of 30 to 33 degrees is the steeper. This difference is probably due to the presence of a slight vegetal cover or to a moderate amount of cementing in the mass which makes the windward part more resistant to the eroding wind than is the case with freshly deposited material.

Not infrequently the desert profiles are made more complicated by the presence of a distinct stratum of more resistant material, which is swept clean by the wind and caps the underlying mushroom-shaped pillars. These usually show clearly by their form the direction of the wind.

Striated Surfaces. Much of the desert surface is strongly striated and grooved. Except in a broad sense it cannot be said to be planed because there are many sharp irregularities on it and it thus differs somewhat from a striated glacial pavement. There are slight local variations in the direction of the striæ but they fall almost wholly between S 65 W and S 70 W. The character of the striated surface is well shown in Figure 4.

Tilted Blocks. None of the features of the desert is more striking than the tilted blocks which lie on its surface. These are most commonly discoid residuals of basalt which have been unearthed by the wind. As they lie on the surface they afford considerable protection to the underlying geest and come to stand on low elongate mounds of which the major portion extends to the leeward in the form of a lee prismoid as described below. During the long period of erosion from the time the upper surface is exposed until the blocks come to stand above the surrounding surface they are modified by the formation of a rain-pitted surface which is somewhat more nearly plane than the under surface and rather well separated from it around the annular rim of the discoid. As erosion continues the windward side of the elongate pillar is con-

stantly undermined and in time the discoid becomes tilted forward toward the wind. In some instances the fall is violent enough so that the residual is displaced and rolls to some random position on one side but a large enough proportion of them assume a definitely oriented and tilted position to form a conspicuous element in the desert landscape.

After the discoid has fallen forward somewhat and lies with its pitted surface toward the wind it lies enough lower than it did before so that a small amount of material is deposited a little distance ahead of it and scour takes place immediately in front of, and behind it. See Figures 5 and 6.

Lee Prismoids. Closely related to the tilted blocks are the prismoidal pedestals which lie to the leeward. These taper to a point both in vertical and horizontal section and represent the form of least resistance to a moving fluid just as does the shape of most fishes or of properly constructed boats. The length is commonly three to four times the width and height, the latter two being commonly about equal. Similar prismoids which are usually much more closely controlled by the shape of the protecting stone are formed of sand behind small stones that lie on the surface.

Lag Materials. All over the surface of the desert one sees the effect of constant sorting by the wind and the resulting accumulation of lag materials which represent for the time and place too great a load for effective removal by the wind. Some of these fragments are large like the tilted blocks. Others consist of small angular and sub-rounded fragments of the weathered rock which accumulate in low or protected places on the surface. (Figure 7). These range from a centimeter or two in diameter down to those of sand sizes.

CHEMICAL DEPOSITS

Secondary Calcium Carbonate. In those parts of the desert which are scoured bare by the wind there are seen in the weathered basalt many calcareous joint fillings and nodular masses of calcium carbonate which have been deposited secondarily in the interstices of the basalt mass. The latter appear in some places to fill the spaces in old masses of basalt. Commonly these are somewhat more resistant to the wind than the basalt geest and stand above the surrounding surface as slight mounds.

Plant Moulds. It is impossible to tell how much of the lime in

the above-mentioned joint fillings has come from the basalt in the process of weathering and how much from overlying masses of calcareous dune sand which have at one time or another occupied every part of the desert strip. At any rate in places which have been recently abandoned by the sand formations there are abundant moulds of plant stems and roots. These are commonly still standing with additional broken parts strewn over the surface. Not uncommonly the stem moulds stand above an old geest surface with parts of the sand formations still lying on it and the root moulds eroded at the margin of the geest surface and lying below it. In these places a few prostrate branches lie in place close to the geest surface and the moulds of what appear to have been extensive vine systems cover the same surface. These are merely rough external moulds of the plant parts and show no structure. The more compact, travertine-like part lies next the inner wall and the outer parts are more porous and carry loosely-cemented layers of the sand which formerly surrounded them. It appears that the cementing was achieved by waters carrying calcium bicarbonate which passed downward through the sand formations as they became stabilized and found the most favorable routes along the stems of plants. It is possible also that some chemical reaction between the decaying stems and the groundwater solutions favored deposition of the calcium carbonate. In places at least the calcium carbonate which appears in the superficial layers of the geest must have come from the leaching of the overlying sand formations.

ABRASION FEATURES

Rock Striation. The striation of the geest surface has been described. In addition at various places in the desert strip but particularly toward the west end where rock fragments which retain a fixed position are more abundant the rock surfaces are distinctly striated by the action of the wind-drifted sand. The striation is best shown on the somewhat weathered surfaces of basaltic spheroids which are partly uncovered by the wind but are still in place and subject to persistent abrasion in one position. In such favorable situations a few rocks appear to have been cut away by abrasion to the extent of several millimeters or perhaps a centimeter or two. The resulting surfaces are rounded in a direction transverse to the wind but tend to be composed of straight line elements parallel to the wind and rising at angles

of ten to twenty degrees toward the leeward. The striate character of the surfaces is fairly clear but differs from a glacially striated surface in that the whole surface is made up of fine groovings rather than of a planed surface marked with scratches. The direction of the individual striæ is subject to slight variation particularly where harder nodules or olivine crystals in the basalt project and deflect the wind currents. Similar results are produced by small pits and vesicles in the surface, from which the striæ radiate in a narrow spray or fan-shaped pattern. (Figure 8.)

Etching. Comparatively little differential abrasion or etching takes place in the basalt under the action of the wind because the rock for the most part is relatively uniform in hardness. In a few places olivine crystals are left protruding as the surrounding rock is worn away.

Polishing. A few of the pieces of dike rock which have been dropped by the Hawaiians are well smoothed and slightly polished but by far the largest part of the abraded surfaces are dull. It is probable that the minerals in the basalt are not favorable to receiving and retaining a bright polish. The fragments of secondary calcium carbonate which are found on some parts of the desert strip are moderately well polished and the sand itself is commonly composed of bright, smooth grains.

Windward Frosting. Some of the blocks of rock which are striated on the top and lateral sides show on their windward sides a rougher, lighter-colored and unstriated surface which may be described as frosted. This surface appears to be due to the impingement of grains of sand where the wind blows so directly against it that the sand is not deflected wholly around the sides or over the top to produce the striated type of surface.

Sand Blasted Pebbles. In a situation such as that being described one expects to find sand blasted pebbles but actually they are surprisingly rare. A few are found which bear the marks of considerable abrasion and have forms approaching to the two or three-angled sharp-crested einkanter, dreikanter, etc., which are found elsewhere. None of these has strongly carved facets or strikingly sharp edges.

Inferiority of Abrasion by Calcareous Sand. The abundance of features attributable to the blowing of the wind combined with the restriction of the marked effects to the weathered geest and to the superficial layers of harder parts of the basalt leads to the

conclusion that the calcareous sand must be vastly inferior as an abrasive agent to the quartz sand which is common in most regions where wind abrasion is impressive. There would perhaps be little difference in the work of quartz and calcareous grains of the same shape on such material as the softer layers of the geest. On the harder rock fragments which lie on the desert there is little doubt that the calcareous sand is confined in its effects to moderate abrasion and slow polishing where quartz under similar vigorous wind action would achieve a much more vigorous carving of the rocks.

Discoid Shapes. Many of the larger basalt fragments which lie on the surface of the desert strip are the cores of units of spheroidal weathering. Some of these are nearly spherical but the bulk of them are oblately spheroidal or lenticular in form and show a considerable differentiation between the top and bottom surfaces. It is not to be understood that the cross section of these as viewed in the direction of the short axis is always circular. There is considerable variation but a strong tendency toward the typical form which is here described. The upper surface of the two is the least convex and is commonly pitted from the weathering which is favored by retention of rain water in initial hollows of the surface. In the most marked examples this pitting covers the entire upper surface, the pits being separated by relatively sharp crested rims. The lower surface is a convex one more nearly of the curvature of the annular profile and is developed on more deeply weathered basalt. On the upper surface the weathering is cleaner and the basalt more nearly fresh. Between the two surfaces is a more or less distinct annular rim which represents the surface of the ground at the time when the distinctive form was developed with the discoid block in a half-buried position. See Figure 5.

SURFACE MARKINGS ON SAND

Ripple Marks. Ripple marks are common on the tops and sides of the dunes and on the sand of the beach. Changes in the direction or strength of the wind commonly lead to alteration of the ripple marks, which as a consequence show the relics of one series being replaced by another. At one place were some large ripple marks of about a foot across, the crests of which had been planed off by the wind and made the site of a smaller series of marks.

Swing Marks. These are common in the sandy parts of the desert as they probably are in sandy regions in all parts of the world. So far as the writer knows no name has been applied to them and the name swing mark appears to be as good as any. They are formed by the swinging to and fro or round and round of stems or roots of plants which are anchored at one or both ends. The commonest form is produced by a grass stem which is broken over at the surface of the sand but not quite broken off. As this lies on the sand the wind sweeps it back and forth around the attachment pivot making marks on the sand in the form of a sector of a circle. If it swings through the full circle a target-like series of marks is the result. A more unusual form is produced when a slender, flexible root which is anchored at both ends is set in motion. This produces a shaded double convex lenticular pattern. See Figure 10.

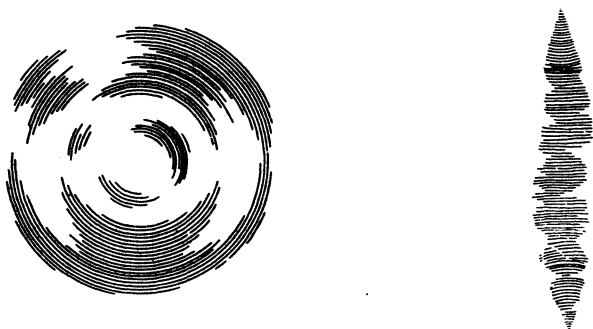


Fig. 10. Sketch of different forms of swing marks developed on sand by wind-swung stems and roots of vegetation.

Pebble Roll Marks. These are irregular discontinuous marks similar to those made by rolling a large snowball and are produced by the rolling of any small objects down steep slopes of the dunes.

Columnar Cliffs in Sand. These are produced by gravity sapping wherever the wind or any other agent has produced a vertical wall of a few inches or feet in sand which is wet or slightly cemented. The columnar configuration is produced by the faithful reproduction vertically of every irregularity in the lower part of the bank. At the bottom of such a columnar bank is commonly a series of merging talus cones made up of the material derived from the bank.

Tracks of Animals. Among the ephemeral features of the desert strip are the tracks of various animals. All those which are plain are in the sand since only the cattle and horses are heavy enough to make a recognizable track in the geest surface. The tracks of cattle were most abundant but those of horses, goats, cats, mice, birds, and various insects were noted.

HUMAN RELICS

Stone Implements. The ancient Hawaiians were skillful workers of stone and many evidences of their work may be found in the desert strip at the present time. The stone implements are not now so abundant as they once were but a few may still be collected. The most common implement is the adze which was made of very compact, fine-grained dike rock by chipping and rubbing. The bulk of those seen by the writer were blanks on which the larger part of the necessary chipping had been done but none of the rubbing. There is a close association between the adze blanks and all the other relics described in this section. They are found strewn over small areas of fifty or a hundred feet in diameter. Commonly they are close to the base of one of the low sand mounds which stand on remnants of the original geest surface. In a few places the relics lie on a geest surface and appear to have been covered with sand and then re-excavated by the wind. There is no convincing evidence however that the bulk of the Hawaiian relics were left on the desert strip at a time prior to the formation of the greater part of the modern sand dunes. It may well be that some were but the most of the material which lies about is probably not more than two or three hundred years old.

Far more abundant than the adzes and rough blanks are the chips and spalls which were produced in working them. These are identifiable both by their lithologic characters and the artificial shapes and freshness of some of their surfaces. It is possible that a few of the chips are from local rock of the discoid residuals but the majority come from a series of dikes near the coast north of the desert. There is a fairly distinct train of this material by which it may be traced back from the desert to the quarry from which the Hawaiians took it.

It is probable that the activity of the Hawaiian stone workers in this area extended over a period of many generations for some

of the chips show at least two generations of etched surfaces. The first appears to have been developed on fragments of the adze rock which were dropped by the earlier carriers. Chips were then broken off these pieces as they were utilized by later generations for adzes. These chips are in turn etched by the wind-driven sand on the fresher faces. There is a distinct difference between the older and newer etched faces.

Marine Shells. Shells of pelecypods of various species and of several species of gastropod are scattered near the artifact materials. Most of these probably were used for food but there is one exception which furnishes clear evidence of human agency in transporting them from the sea coast. These are the cowrie shells (*Cypræa tigrina*) which are used as bait in squid fishing. These invariably have one side of the opening chipped out as is necessary to admit the straight stick which is inserted between the sinker proper and the shell.

Smoothing Pebbles. Small, very smooth pebbles, probably of beach origin in the first place, are used as smoothing stones in rubbing and polishing articles of wood and others were probably used in cooking small birds. All these are abundant round the artifact sites. In addition to these small pebbles there are a number of large beach cobbles of a somewhat elongate form and 20 to 40 centimeters in their longest diameter. These are rather symmetrical and were probably used for hammering and as anvils. (Figure 9).

Coral Files. A few fragments of rough coral which are shaped to a triangular wedge form are the files used in sharpening fish-hooks and in cutting away other materials. Near the various relics mentioned in a few places were found the remains of small fire places in which a few fragments of charcoal are still to be found.

HISTORY OF THE DESERT STRIP

ORIGIN

The desert strip owes its existence to the action of the wind-driven sand in killing vegetation by abrasion and by burial. Though the west end of Molokai is dry and shows at various other localities the evidence of much work by the wind, the extreme development of strongly oriented eolian features is confined to the strip which extends in a straight line with well defined parallel

sides across the upland. The sand is derived from the beach at Moomomi and is being formed today by wave action on the small living reef which lies off shore at this point. At the present time very little sand serves to keep vegetation down for the strip is now so deeply abraded that the exposed deeper geest is relatively unfavorable for plant growth.

HISTORY

Little is known which enables one to make an estimate of the age of the desert strip. The great mass of eolian sandstone which forms a headland just west of Moomomi beach was probably formed when the coast was less eroded and the land extended several hundred yards farther north than now since it could hardly have been formed by the blowing of sand from a beach having the location of the present one. The larger part of the old well-cemented sandstone on the upland lies to the north of the present strip and likewise suggests that sand had at an earlier time better access to the northern upland than now. Considering the amount of coastal abrasion which appears to have taken place and the cementing and weathering of the sandstone the origin of the desert strip may well be dated some tens of thousands of years ago.

At any rate it is clear that during the earlier part of its history it extended farther both to the north and also to lesser extent farther to the south than it does at present. Whether both of these greater extensions took place at the same time so that the desert was appreciably wider than now is not known but is thought to be probable. It is difficult to tell whether the desert strip was so long and continuous toward the southwest in the earlier part of its history as it now is because the southwest end of the desert once reclaimed would not carry as permanent marks of its old desert character because of the lesser quantity of sand which lies on it. Evidence of a broader desert strip are confined to the northeast slope and the summit portion and do not continue far to the southwest. With the abandonment of active sand drifting in the sections marginal to the present strip the desert assumed a regimen which was essentially that of today. Probably the earlier part of the history including the cementing, weathering and erosion of the oldest of the sand formations was very much longer than the later part during which the sand has been confined essentially to the present strip.

During this later period two fairly distinct formations of sand have been formed. So far as known only the latter is contemporaneous with Hawaiian occupation of the island. The locations of the fire places and other groups of relics are such as to suggest that the topography, even to the details of the sand mound remnants and tilted blocks, was substantially the same when the Hawaiians left them. The more recent activities of stone working Hawaiians are no more than 100 years in the past but the testimony of different stages in the etching of artifact chips is to the effect that the earlier Hawaiian work here may be several hundred or a thousand years old.

IMPORTANCE OF WIND EROSION

We may therefore conclude that the formation of some of the smaller features of the desert such as the sand-covered geest remnants or even the excavation and tilting of the tilted blocks may represent the work of several hundred years. The average amount of material removed by wind erosion in the desert was not ascertained with any degree of precision but by way of illustration we may take five feet as a reasonable figure. If the total age of the desert strip is estimated at 50,000 years this will amount to an average removal of one foot in 10,000 years. The principal value which attaches to a rough estimate of this sort which may well vary two or three fold either way from the truth is to indicate the relation of wind erosion under local and very favorable conditions to the rate of stream erosion. The figure given indicates that the rate of wind erosion may locally and under very favorable conditions approach the average rate of reduction of large continental masses by streams. The special conditions here with the continuous supply of sand which enters in no way into the computation of quantities removed must indicate the very slight quantitative importance of wind erosion in general as compared to stream erosion.

At the same time where conditions are relatively unfavorable to stream erosion wind erosion is capable of producing a large series of striking and typical topographic forms and details which quite dominate the landscape. At no place is this more strikingly shown than in one such as described above where strong trade winds blow persistently from one direction throughout the year.



Fig. 4. Detail of striated horizontal surface of the desert. Part shown is about two feet long. Direction of wind is from left to right.

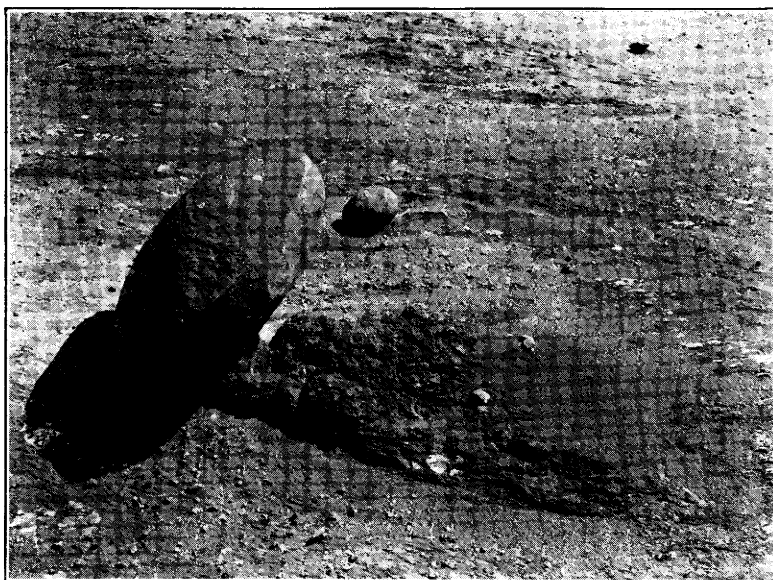


Fig. 5. View of tilted block showing discoid form and pronounced annular rim between upper and lower surfaces.





Fig. 6. View of tilted blocks showing rude discoid forms, pitted upper surfaces and elongate pedestals.

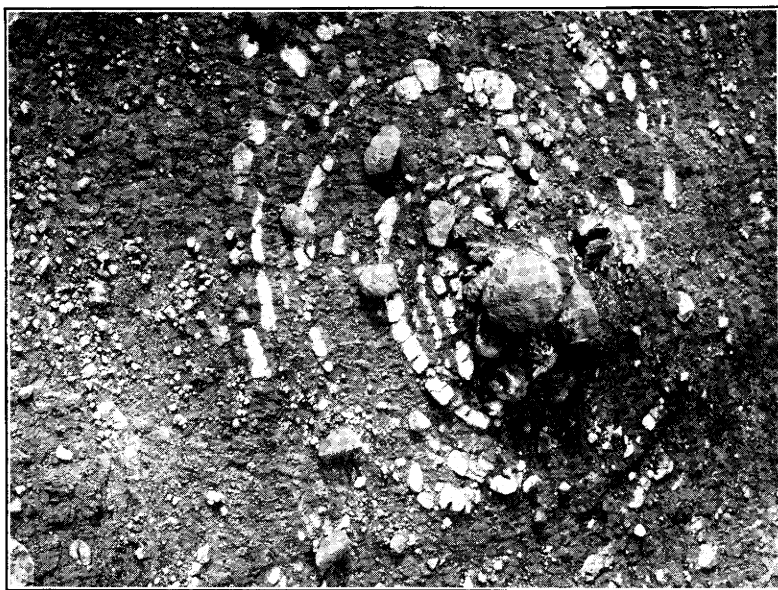


Fig. 7. Detail of desert surface showing cross section of spheroidal structure of basaltic geest which lies beneath. Loose fragments on the surface are loosened by plucking and uncovering by the wind and then become abraded and worn down to the harder stone.

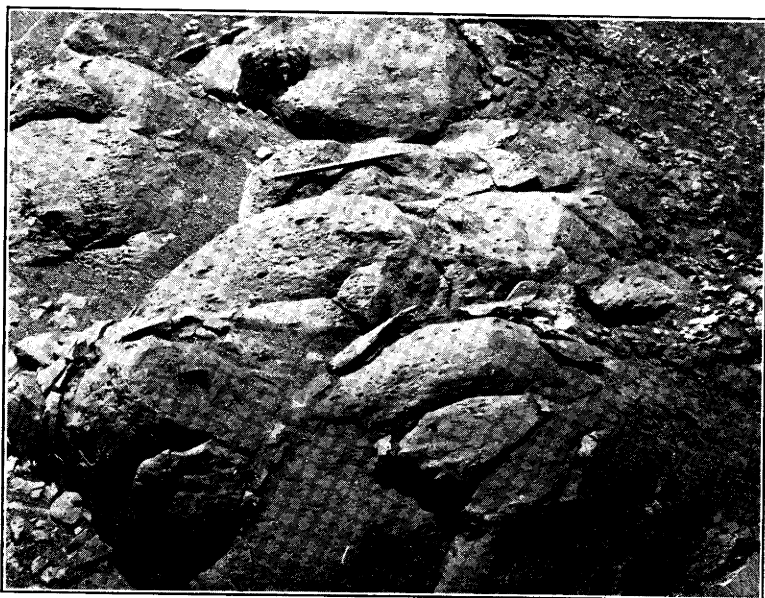


Fig. 8. Detail of abraded and striated rock surfaces. Pencil points in direction wind moves.



Fig. 9. Detail of desert surface showing large rounded beach pebble and artifact chips left by Hawaiian natives.

UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

VOLUME XI

NUMBER 5

PAPERS ON THE PRAIRIE

by

B. SHIMEK

PUBLISHED BY THE UNIVERSITY, IOWA CITY

THE PERSISTENCE OF THE PRAIRIE

B. SHIMEK

The belief that the prairie flora will not return if the prairie is broken is widely prevalent. With it is linked the further belief that the prairie flora is not a climax flora, but that it represents a transition stage which would culminate in a forest with the cessation of prairie fires, were it not for the disturbance of the prairie surface by cultivation.

It is true that the prairie yields readily to cultivation. The breaking of the prairie turf is sufficient to cause most of the prairie plants to disappear from the broken surface, but there is abundant evidence to show that it requires continued cultivation to keep them out. Their return is rather slow and is preceded by a transitional mixture of species, but it is quite certain, provided man does not interfere.

Comparatively little of the native prairie remains in Iowa. A few unbroken tracts are still scattered about over the state, especially in the northwestern quarter, but even these have been disturbed more or less by pasturing and cutting. The purest remnants of the prairie are often found along the right of way of the older railways which entered the territory before the original prairie was broken, and they give the most striking illustration of the persistence of prairie where it remains undisturbed, even in such narrow strips as those here noted.

In this state the prairie flora survives in these unbroken areas, and also in neglected corners, along fence-rows, in partially pastured areas, and on more or less undisturbed open grounds generally. Much of this native flora was also formerly preserved along the public highways, but this is rapidly disappearing with the widening of the driveways on the primary roads and the enforcement of the unwise indiscriminating weed-laws of the state along secondary roads.

These various remnants of the prairie flora are widely scattered, and they are amply sufficient to re-seed all suitable areas. No native prairie species has entirely disappeared, though all have been much reduced, and in a few cases almost exterminated. Perhaps the most striking of the latter kind is that of one of the blaz-

ing stars, *Liatris squarrosa*, once abundant on the prairies of Iowa, but now very rare. The buffalo grass, *Buchloe dactyloides*, never common in Iowa, is now almost, if not entirely, extinct. Other species have become very rare, but on the whole the original prairie flora is practically preserved, and if given an opportunity it would no doubt again spread over a large part of the state. It has even advanced into many places which were formerly covered with forest, but in such cases the prairie flora persists only when the return of the forest is artificially prevented. Numerous illustrations of this fact are found where the railway right of way has been kept cleared through the groves which broke the monotony of the prairies in Iowa. In such cases the prairie usually invades the denuded areas, in which it will probably persist so long as the right-of-way is kept clear. Some years ago the writer reported¹ a similar case, where prairie took possession of the borders of a road cut through the forest north of Homestead, Iowa, and periodically cleared for many years. The borders of this road have not been cleared since, excepting as the driveway has been widened and graded, and most of the prairie flora is being crowded out by the rapidly returning forest flora.

For many years the writer has been engaged in making field-observations on the development and disappearance of prairie floras, and this paper contains an account of such changes in two widely separated areas, the result in each case being the return of the prairie flora to a disturbed surface.

The first of these areas extends along the Chicago, Rock Island and Pacific Railway between Wilton and Summit, in Muscatine County, Iowa, and illustrates both the persistence of the prairie flora on undisturbed surfaces, even when narrow, and the possibility of the return of this flora to disturbed areas.

The second is a more limited area adjoining Mason City, Iowa, and illustrates a result of the invasion of a formerly cultivated area by the prairie in apparent competition with a forest flora on the opposite side.

I. THE WILTON-SUMMIT AREA

This area embraces the right of way, averaging less than one hundred feet in total width, along the Wilton and Muscatine branch of the Chicago, Rock Island and Pacific Railway, beginning at a point nearly half a mile south of Summit and extending to the for-

¹An artificial prairie.—This Bulletin, vol. VI, no. 4; 1913.

est border south of Wilton, a total distance of about five miles. The area is shown within the three two-mile stretches represented in Plate I.

This line was constructed in the year 1854, when most of the surrounding region was uncultivated, and strips of the original prairie still remain within the right of way. The portion of the line here considered traverses a high prairie, lying entirely within a gently undulating Illinoian drift plain (Plate II, fig. 1). In the report on Muscatine County, Udden² represents this area as loess-covered, but there is no loess in the part of the plain under consideration. Most of the area is covered with a fertile prairie loam, but the ridges often show some sand,—evidently small outliers of the old sand-dune area bordering the Cedar River valley to the west.

The undulating character of the surface is well shown along the railway, necessitating a succession of rather low cuts and fills, as shown in Plate I. The depressions are more or less swampy, and are covered with a hydrophytic flora, while the better drained areas are occupied by a more or less xerophytic prairie flora.

The road-bed and the ditches on either side occupy about 25 feet of the width of the right of way, but in some places there has been a further disturbance of the surface by the deeper cuts (which extend to the edge of the right of way in several places), by the heaping up of ridges of earth excavated from the cuts, or by additional grading to secure earth for the fills. Excepting for these interruptions, and those caused by the intersecting public highways at intervals of a mile, the outlying strips on both sides of the right of way form continuous belt transects of the original prairie about five miles in length and reaching a width of more than thirty feet in the widest place.

The entire right of way therefore presents three more or less distinct surface types: 1. The outlying original prairie belts on either side, with the native prairie flora well preserved. 2. The areas disturbed early in the history of the road by cuts, or ridges thrown up from the cuts, but subsequently practically undisturbed for many years, to which the prairie flora has fully returned. 3. The road-bed proper with its ballast and the bordering ditches, all of which are subjected to frequent disturbances in connection with the repair and maintenance of the railway. The flora of this section is mixed, and contains a large element of introduced weeds.

²Iowa Geological Survey, vol. IX; 1899.

1. The Original Prairie

The remarkable tenacity of the prairie flora is well illustrated in these belt transects of unbroken prairie. For many years the adjoining fields have been under cultivation, and both fields and fence-rows have produced weeds abundantly. On the inner side each belt transect has been in contact with the middle roadbed belt, with its numerous weeds and other introduced plants. (See more detailed discussion of the flora of this belt under section 3, following.) Yet few introduced plants have been able to establish themselves in the belts of unbroken prairie, and most of these in very small numbers. The blue grass, *Poa pratensis*, seems to make the most successful invasions, but does not establish a sod to the exclusion of the native prairie plants, and it is probable that its success is due in large part to the frequent introduction of new seed. *Poa compressa* is less frequent, and usually occurs in areas which have been somewhat disturbed. It is possible that this was a native of the drier prairies. Two other introduced plants occasionally gain a foothold, but usually in very small numbers. They are timothy, *Phleum pratense*, which is also extensively cultivated on the farms, and asparagus, *Asparagus officinalis*, which is also commonly cultivated. In the latter case birds which feed on the berries are evidently responsible for the wide dispersal of the seeds.

Aside from these four by no means conspicuous invaders these belts contain a typical prairie flora where the surface has not been disturbed, or where it does not become very wet during the early part of the season.

Where there have been minor local disturbances of the prairie turf by gophers, groundhogs, slight excavations for earth needed for ballasting the track, etc., the disturbed surface is usually promptly invaded by a mixed group of plants consisting in part of introduced foreign weeds and in part (or originally, and sometimes even now entirely) of certain native prairie plants which now also invade cultivated grounds and pastures, and which were evidently the "weeds" of the original prairie which took possession of all disturbed surfaces. These weeds are usually soon followed by the climax flora of the prairie. They are discussed in section 2, Restored Prairie.

The continuity of the prairie belts is also interrupted by the low areas which alternate with the higher places indicated in Plate I

by railway cuts. Some of these depressions are creek-beds, but most of them are undrained. Their flora is that which usually characterizes low areas in the prairie region which are wet during at least a part of the year. There is no larger body of water in this area, and none of the depressions retain water during the average season, hence the flora is marsh rather than aquatic. The following plants of this type were noted:

<i>Typha latifolia</i>	<i>Polygonum Muhlenbergii</i>
<i>Panicum dichotomiflorum</i>	<i>Rumex brittanica</i>
<i>Leersia oryzoides</i>	<i>Rumex mexicanus</i>
<i>Agrostis alba</i>	<i>Radicula palustris</i>
<i>Calamagrostis canadensis</i>	<i>Penthorum sedoides</i>
<i>Glyceria nervata</i>	<i>Saxifraga pennsylvanica</i>
<i>Elymus virginicus</i>	<i>Lythrum alatum</i>
<i>Eleocharis palustris</i>	<i>Ludwigia polycarpa</i>
<i>Scirpus fluviatilis</i>	<i>Oenothera pratensis</i>
<i>Scirpus atrovirens</i>	<i>Cicuta maculata</i>
<i>Scirpus cyperinus</i>	<i>Steironema ciliatum</i>
<i>Carex vulpinoidea</i>	<i>Asclepias incarnata</i>
<i>Carex Sartwellii</i>	<i>Verbena hastata</i>
<i>Carex lanuginosa</i>	<i>Stachys palustris</i>
<i>Acorus calamus</i>	<i>Galium asprellum</i>
<i>Juncus interior</i>	<i>Aster salicifolius</i>
<i>Iris versicolor</i>	<i>Silphium perfoliatum</i>
<i>Habenaria leucophæa</i>	<i>Bidens frondosa</i>
<i>Salix longifolia</i>	<i>Bidens aristosa</i>
<i>Salix cordata</i>	<i>Helenium autumnale</i>

Of this list, *Agrostis alba*, *Habenaria leucophæa*, *Rumex mexicanus*, *Oenothera pratensis*, *Steironema ciliatum*, *Verbena hastata*, *Stachys palustris*, *Aster salicifolius* and *Silphium perfoliatum*, also sometimes appear on drier prairie, but they seem to prefer low grounds.

Where the prairie merges into these lower areas there is usually a mixture of the two floras consisting of the above-noted less hydrophytic forms of the low grounds and the less xerophytic species of the prairie. The latter includes species which are commonly found on the richer, less-exposed parts of the prairie, but also occur not infrequently in wet places. In this region the following species, listed in the table of prairie plants, are of this type:

<i>Carex gravida</i>	<i>Gerardia purpurea</i>
<i>Hypoxis hirsuta</i>	<i>Lobelia spicata</i>
<i>Thalictrum dasycarpum</i>	<i>Liatris pycnostachya</i>
<i>Anemone canadensis</i>	<i>Aster novæ-angliæ</i>
<i>Spiræa salicifolia</i>	<i>Aster paniculatus</i>
<i>Polygala sanguinea</i>	<i>Ambrosia trifida</i>
<i>Gentiana Andrewsii</i>	<i>Rudbeckia subtomentosa</i>
<i>Apocynum cannabinum</i>	<i>Helianthus grosseserratus</i>
<i>hypericifolium</i>	<i>Helianthus tuberosus</i>
<i>Gerardia auriculata</i>	

The following species in the prairie table are restricted in the native prairie transect to the sandy areas on the outliers of old dunes:

<i>Eragrostis pectinacea</i>	<i>spectabilis</i>	<i>Ambrosia psilostachya</i>
<i>Cyperus filiculmis</i>		<i>Helianthus occidentalis</i>

To them should be added *Lechea stricta*, *Viola pedata*, *Asclepias amplexicaulis* and *Lithospermum Gmelini*, which occur in similar situations but are less common.

The table of prairie plants contains 16 species which are not represented in the prairie transect. All of these species occur on the prairie of the general region, but they were not found within the limits of the transect. It will be observed that one-half of them are prairie "weeds" (see 2, Restored Prairie), and also include *Phleum pratense*, an introduced species which occurs sparingly on undisturbed prairie.

The entire native prairie transect presents a very characteristic prairie flora, comparable in its composition and variations to that of any larger prairie area in this part of the state.

2. Restored Prairie

The restored prairie appears upon two types of surfaces,—the larger fills and the sides of the cuts. (For location of these see map, Plate I).

The prairie flora has extended quite generally over the sides of the larger fills, but the proximity of the road-bed with its numerous weeds, and the more frequent local disturbances of the surface caused by section hands working along the road-bed, have resulted in a frequent admixture of foreign invaders.

A much purer prairie flora has taken possession of the slopes of the deeper cuts. When the road was constructed these surfaces were, of course, bare. No record of the invasion and succession of floras in these areas has been preserved, but, judging from the history of more recent exposures of the same kind, as noted by the writer in many cases, the first plants to enter were undoubtedly those enumerated herein as prairie weeds with some admixture of imported weeds. Because of the newness of the territory the latter were probably not very numerous. This flora was gradually replaced until today it is indistinguishable from that of the adjoining native prairie.

Several of these cuts are found along the railway between Wilton and Summit, and they are noted in Plate I.

Those within the first mile are located chiefly in the southern half, and do not exceed 5 feet in depth.

The second mile contains two cuts. Cut a begins about 200 yards south of the north end of the mile and extends southward for about one-half mile. It reaches a maximum depth of 11 feet, and its slopes present a fine example of restored prairie. This also extends over the ridges which were heaped up above the sides of a portion of the cut at the time the excavation was made. A portion of this cut is shown in Plate II, fig. 2.

Another cut, b, is located near the south end of the mile. This is about 100 yards long and reaches a depth of 8 feet. The ridge here cut is quite sandy and the flora of both the original prairie transect and the restored slopes show a scattering of the species listed as characteristic of sandy prairie among the ordinary species of the drier prairie.

The third mile is almost flat and shows but one small cut about 3 feet in depth.

The fourth mile contains another fine cut, c, which is more than 450 yards long and reaches a depth of 14 feet. Ridges heaped up above portions of this also show restored prairie.

The fifth mile contains several cuts. Cut d is more than 500 yards long and reaches a maximum depth of 11 feet. Cut e is about 90 yards long and 5 feet deep. A ridge on either side above the cut, about 5 feet wide and two feet high, is now covered with a prairie flora. Cut f is about 180 yards long and 8 feet deep. Its slopes are almost entirely covered with *Robinia pseudo-acacia* which had been planted nearby and has extended to this and portions of other cuts. The *Robinia* is distinctly a tree-weed and does not establish forest conditions.

The cut which is located in the south half of the sixth mile is not included in this discussion. It is located at the edge of the rough, timbered area bordering the Mississippi River, and the railway begins here to drop rapidly into the valley of Mad Creek. Its flora is mixed.

The faces of the cuts a to e, as well as the ridges above the cuts, have remained undisturbed for many years, excepting where gophers or ground-hogs have burrowed, or where limited areas were disturbed by man. They are now covered with a typical prairie flora, which is recorded in the second column of the prairie table. It will be observed that 112 species are common to these areas and the native prairie transect.

So complete is the extension of the prairie flora over the once disturbed surfaces that there is no way of determining their limits on the prairie side excepting by the upper edges of the cuts and the bases of the ridges which had been piled up on the prairie bordering the cuts.

The 39 species which were found on the native prairie (recorded in the first column) but not on the restored areas, are rare or local on the prairie of this region. Several, like *Agropyron Smithii*, *Hordeum jubatum*, *Oxybaphus nyctagineus*, *Silene antirrhina*, *Hypericum cistifolium*, *Ellisia nyctelea* and *Physalis pruinosa*, are prairie weeds which occur upon the disturbed spots within the restored prairie, but have not been observed on the older portions. Several others, like *Carex scoparia*, *Lilium philadelphicum andinum*, *Thalictrum dasycarpum*, *Anemone canadensis*, *Polygala sanguinea*, *Gentiana Andrewsii*, *Gerardia auriculata*, *G. purpurea*, *Rudbeckia subtomentosa* and *Helianthus tuberosus*, are ordinarily found only upon rather moist prairie, and these drier restored areas would not offer a congenial habitat. The remaining 22 species are quite rare even in the larger native prairie areas of this tract, and their absence in the more restricted restored areas is not surprising.

The great bulk of the flora is the same on both types of areas, and there is practically no admixture of weeds or other foreign plants in either, excepting where there have been local disturbances of the surface, as noted.

These disturbed places in either area are promptly occupied by a mixture of prairie weeds, imported weeds, and later the plants of the permanent prairie. The plants here designated as prairie weeds play an important part in this succession, as they are among the first to take possession of surfaces which have been disturbed sufficiently to break up the prairie turf. Since the invasion of our territory by a large number of foreign weeds the latter join with the prairie weeds in covering new surfaces, but on the original prairie the prairie weeds evidently formed the first transitional flora, later to be replaced gradually by the climax prairie flora. The prairie weeds also appear on native prairie, but they are usually the first to enter broken areas.

Since the breaking of the prairies these prairie weeds have entered the cultivated fields and most of them have become noxious weeds. They are also likely to invade waste places, especially if sandy or rather barren. Thirty such species were found on the

disturbed portions of the prairie under discussion. They are marked with the letter x in the prairie table.

3. The Roadbed

The middle strip includes the roadbed and the lateral drainage ditches, and is subject to frequent disturbances by the section-hands whose duty it is to keep the roadbed in repair. The ditches frequently contain marsh plants of the species already noted, and need no further attention here.

The roadbed includes the area between the rails, and a strip on either side from 3 to 5 feet in width. A portion of it is well shown in Plate II, fig. 2. Its flora is a mixture and is derived from the following sources:

From prairie.—A large part is derived from the prairie and is recorded in the third column of the prairie table. It includes the four introduced species and the thirty prairie weeds, most of the latter being rather common. Many of the remaining prairie species are represented only by scattered individuals. The low form of *Rhus Toxicodendron*, elsewhere occurring on the prairie, is also found here. This makes a total of 130 species of prairie plants observed on the roadbed.

From dry open places, etc.—The following roadbed species were evidently introduced from dry borders of thickets and open places:

Bromus purgans	Aster sagittifolius
Rubus villosus	Gnaphalium polyccephalum
Hypericum Ascyron	Erigeron annuus
Apocynum androsæmifolium	

From sand-ballast.—The roadbed is ballasted in part with sand brought from the Cedar River valley. The following species occurring on the roadbed were evidently introduced with the sand:

Paspalum ciliatifolium	Tephrosia virginiana
Cenchrus carolinianus	Astragalus distortus
Aristida gracilis	Strophostyles helvola
Sporobolus cryptandrus	Strophostyles pauciflora
Eragrostis pectinacea spectabile	Oxalis filipes
Eragrostis Frankii	Croton glandulosa septentrionalis
Festuca octoflora	Oenothera rhombipetala
Hordeum pusillum	Asclepias amplexicaulis
Cyperus Schweinitzii	Verbena angustifolia
Carex setacea ambigua	Plantago aristata
Polygonum tenue	Plantago Purshii
Frælichia floridana	Pentstemon hirsutus
Mollugo verticillata	Antennaria neglecta
Draba caroliniana	Xanthium commune
Polanisia trachysperma	Helianthus petiolaris
Crotalaria sagittalis	

It is also probable that most or all of the plants of *Aristida basiramea*, *Cyperus filiculmis* and *Helianthus occidentalis*, noted in the prairie table, were introduced with the sand ballast rather than from proximate sandy prairie.

From wet places.—The following species of swamp plants were represented on the roadbed chiefly by scattered individuals. They were probably derived from the adjoining ditches.

<i>Panicum dichotomiflorum</i>	<i>Polygonum Muhlenbergii</i>
<i>Agrostis alba</i>	<i>Apios tuberosa</i>
<i>Muhlenbergia mexicana</i>	<i>Rotala ramosior</i>
<i>Spartina Michauxiana</i>	<i>Cornus stolonifera</i>
<i>Carex lanuginosa</i>	<i>Steironema ciliatum</i>
<i>Carex tetanica</i> Mead.	<i>Verbena hastata</i>
<i>Salix longifolia</i> (juv.)	<i>Stachys palustris</i>
<i>Rumex brittanica</i>	<i>Aster salicifolius</i>
<i>Rumex mexicanus</i>	<i>Silphium perfoliatum</i>

From the forest.—The forest has contributed several species to the roadbed, but chiefly near the northern end where the grove along the creek probably constitutes the chief source. This grove is composed of such species as *Acer saccharinum*, *A. Negundo*, *Salix amygdaloides* and *Betula nigra* in the lower parts, and *Ulmus americana*, *Celtis occidentalis*, *Juglans nigra*, *Gleditsia triacanthos*, *Fraxinus pennsylvanica lanceolata*, *Carya cordiformis*, *Crataegus mollis*, *Prunus serotina*, *Tilia americana*, *Populus tremuloides*, *Quercus velutina*, *Q. macrocarpa*, etc., and contains the usual accompanying smaller species of our alluvial woods and banks.

The following forest species were found on the roadbed, mostly in very small numbers and not far from the grove:

<i>Smilax herbacea</i>	<i>Geranium maculatum</i>
<i>Polygonum scandens</i>	<i>Psedera quinquefolia</i>
<i>Physocarpus opulifolius</i>	<i>Cornus paniculata</i>
<i>Rubus allegheniensis</i>	<i>Sambucus canadensis</i>
<i>Rubus occidentalis</i>	<i>Erigeron annuus</i>
<i>Prunus virginiana</i>	<i>Cacalia suaveolens</i>

These species do not appear constantly, but form a fluctuating and inconspicuous element of the flora. It will be noted that most of them produce fleshy fruits, and birds are probably responsible for their appearance on the roadbed. The remaining species could easily be distributed by wind or moving trains.

The seedlings of the following trees have also been found from time to time:

<i>Populus deltoides</i>	<i>Prunus ioensis</i>
<i>Ulmus fulva</i>	<i>Robinia pseudoacacia</i>
<i>Celtis occidentalis</i>	<i>Gleditsia triacanthos</i>
<i>Quercus macrocarpa</i>	<i>Acer Negundo</i>
<i>Prunus serotina</i>	<i>Acer saccharinum</i>
<i>Prunus americana</i>	<i>Fraxinus pennsylvanica lanceolata</i>

None of these seedlings occur in large numbers, and though they have been observed for a number of years, none seem to become established. Wind and birds are probably responsible for their recurrence.

It is possible that some of the seedlings of the species of *Populus*, *Ulmus*, *Acer* and *Fraxinus* are derived from trees cultivated near the farm-houses. It is quite certain that this is the source of the thickets of *Robinia* which occupy parts of the disturbed surfaces near Summit, and seedlings of which sometimes appear on the roadbed. This species is not a native of the region.

Introduced weeds.—Mingled with the plants of the preceding lists are numerous species of weeds which are not native to this part of the state, or have become so thoroughly established as weeds that their source cannot be determined definitely. They have been introduced chiefly by gradual diffusion or by the railway with stock and produce, though wind, birds and other agencies may have assisted. It is noticeable that the most persistent of these weeds are usually most abundant near the railway stations, this being true of this area as well as of the state at large.

The introduced weeds may be considered in two groups: those which are native to our country, and those which are of foreign origin.

The group of American weeds includes a number of species which may be native to this part of Iowa, but they are now so generally distributed as weeds that they are included here. With one possible exception they cannot be regarded as members of the prairie flora, though most of them occasionally appear upon slightly disturbed portions of the prairie. The list follows:

<i>Panicum capillare</i>	<i>Euphorbia maculata</i>
<i>Humulus lupulus</i>	<i>Verbena bracteosa</i>
<i>Polygonum erectum</i>	<i>Teucrium canadense</i>
<i>Polygonum pennsylvanicum</i>	<i>Solanum carolinense</i>
<i>Amaranthus blitoides</i>	<i>Solanum nigrum</i>
<i>Lepidium virginicum</i>	<i>Solanum rostratum</i>
<i>Sisymbrium canescens</i>	<i>Physalis subglabrata</i>
<i>Oxalis corniculata</i>	<i>Veronica peregrina</i>
<i>Acalypha virginica</i>	<i>Plantago Rugelii</i>

Perhaps *Sisymbrium canescens* and *Plantago Rugelii* should be included in the prairie weeds list, as both are natives of the prairies of Iowa. The former, however, seems to be restricted to waste and disturbed places in this region, and the latter has become so thoroughly established as a weed that it is often much more abundant than the introduced *P. major*.

The foreign weeds of the roadbed are mostly of common and widely distributed species, of which two, *Bromus tectorum* and *Melilotus alba*, are increasing rapidly. The list follows:

<i>Digitaria sanguinalis</i>	<i>Sisymbrium officinale</i>
<i>Echinochloa crus-galli</i>	<i>Sisymbrium altissimum</i>
<i>Setaria viridis</i>	<i>Sedum purpureum</i> (rare)
<i>Setaria glauca</i>	<i>Trifolium procumbens</i>
<i>Bromus tectorum</i>	<i>Melilotus alba</i>
<i>Lolium italicum</i>	<i>Melilotus officinalis</i>
<i>Cannabis sativa</i>	<i>Pastinaca sativa</i>
<i>Rumex crispus</i>	<i>Nepeta cataria</i>
<i>Rumex acetosella</i>	<i>Verbascum thapsus</i>
<i>Polygonum aviculare</i>	<i>Anthemis cotula</i>
<i>Polygonum convolvulus</i>	<i>Aretium minus</i>
<i>Chenopodium album</i>	<i>Taraxacum erythrospermum</i>
<i>Amaranthus retroflexus</i>	<i>Taraxacum officinale</i>
<i>Capsella bursa-pastoris</i>	<i>Lactuca scariola</i>
<i>Brassica arvensis</i>	<i>Lactuca scariola integrata</i>

To this list may be added the following small group of species which have escaped from cultivation and some of which have become weeds, particularly those in the second column:

<i>Triticum sativum</i>	<i>Trifolium pratense</i>
<i>Zea mays</i>	<i>Trifolium hybridum</i>
<i>Raphanus sativus</i>	<i>Medicago sativa</i>

This interesting mixture of prairie, swamp, forest, and introduced plants represents a condition which is common where new surfaces have been created, and where competition is possible between the floras of the several types. The bars and borders of most of our streams present essentially the same combination of floras, though the percentage of each will vary with the character of the contiguous territory from which they are derived.

The struggle between these floras continues until that one which is best adapted to the region becomes dominant. In the Wilton-Summit region the prairie flora would undoubtedly dominate on the roadbed if left undisturbed, as it has done on the restored prairie surfaces; along the streams the forest would more frequently become dominant; but in either case the earlier mixed character of the flora represents a transition stage which soon yields to the flora best fitted to survive.

The presence of this belt of mixed floras on the roadbed is especially worthy of note because it shows that despite exposure to possible encroachment by the several floral elements here combined, the prairie flora has been able to re-establish itself on the adjacent strips of restored prairie and is holding its own against this varied competition.

An additional interest attaches to the list of native prairie plants in column I because it is the first definite published list of prairie plants from the Illinoian drift of Iowa. Previous lists, published by the writer³ covered portions of the prairies on Kansan, Iowan and Wisconsin drifts.

It is sufficient here to note that the prairie flora of these several drift areas, as of other surface areas in the state whether loess or alluvium, shows no differentiation which would indicate or suggest that surface formation has anything to do with the distribution of the prairies. On the contrary, true prairie, with its characteristic flora, occurs on every type of soil or formation which comes to the surface in Iowa, excepting the muck of swamps, and even that will usually produce prairie if thoroughly drained and left undisturbed.

II. THE MASON CITY TRACT

Another area illustrating the ability of the prairie to return has been studied by the writer near Mason City for a number of years. This case is even more remarkable than that discussed in the first part of this article because of the possibility of sharper competition between forest and prairie.

This area is located between the north line of Highlands Addition to the city and Buffalo Slough, a swampy abandoned channel of Lime Creek. The Slough is bordered by limestone ledges which rise to a height of 35 or 40 feet, and have a prominent rocky forested talus at the base. The forest also enters the gulleys and ravines which cut the line of ledges. (See Plate IV, fig. 1).

The upland above the edges of the ledges rises to a height of 50 feet, or more, above the bed of the Slough. It was formerly covered partly with native prairie, and partly with scattered or interrupted groves which connected more or less with the groves and thickets of the talus and ravines. The area here considered lies on this upland west of the line extending north from the north end of Kentucky Avenue to the Slough. Along this line a strip of native prairie about 40 feet wide and nearly 500 feet long was broken and planted in corn. Along the west side of this strip lies a piece of unbroken prairie, while just east of it is a small upland grove which is a part of the bluffs forest belt.

The cultivation of this strip was soon abandoned, and for about

³Report on Harrison and Monona Counties, Iowa Geological Survey, vol. XX, 1910; The Prairies, this Bulletin, vol. VI, No. 2, 1911; The Plant Geography of the Lake Okoboji Region, this Bulletin, vol. VII, No. 2, 1915.

5 years the writer gave it only passing notice, since it appeared merely as a neglected weed patch. Unfortunately no record of the plants was kept during this period, but at its close more systematic observations were begun and continued for 5 years. At the beginning of this second 5 year period the ridges marking the old cornrows were still plainly visible, but the tract was covered late in the summer with a mass of *Aster multiflorus*, *A. azureus* and *Solidago rigida*, with a scattering of prairie weeds such as *Agropyron Smithii*, *Hordeum jubatum*, *Potentilla monspeliensis*, *Rosa pratincola*, *Hedeoma hispida*, *Erigeron ramosus*, *Ambrosia artemisiifolia* and *Achillea millefolium*; and of introduced weeds such as *Phleum pratense*, *Poa compressa*, *P. pratensis*, *Trifolium pratense*, *T. procumbens*, *Melilotus alba* and *Taraxacum erythrospermum*. The general appearance of this strip was quite different from that of the adjoining undisturbed prairie along the west side. While the two species of *Aster* and the *Solidago* dominated the restored strip, their flowers producing a distinct belt of color, the native prairie presented a much larger number of species, with none so prominent as the three noted in the restored strip, and these three, while present, were scattered and comparatively few in number.

These observations have been continued for 5 years, and in 1924 the number of prairie species had been increased, the species were more equally mixed, the introduced weeds had almost disappeared, and the striking distinction between the restored and native prairie had disappeared. The number of species is still distinctly less in the restored strip, but its flora is clearly of the prairie type and most of the species of the native prairie will no doubt return to it if it is not again disturbed.

A comparative view of the floras of the restored and contiguous native prairie may be obtained by scanning columns V and IV of the Table of Prairie Plants, and, in addition, the supplementary lists which follow.

The following prairie species should be added to both the native and restored prairie lists given in the table:

Agropyron Richardsonii
Lathyrus venosus
Galium boreale

Antennaria plantaginifolia
Brauneria pallida

The following border plants (also found in open woods) were also sparingly represented in both areas:

Bromus purgans

Apocynum androsamifolium

The following species should be added to the native prairie list in column IV:

Vicia americana
Rhus Toxicodendron

Tanidia integerrima
Aster oblongifolius

The *Tanidia* often occurs in borders and open woods; the *Aster* is often found in rocky and barren places; and the *Rhus* is the low form characteristic of the prairies.

The following species were sparingly represented on the restored prairie, and should be added to the list in column V of the Table:

Draba caroliniana
Trifolium stoloniferum

Symphoricarpos occidentalis
Lactuca ludoviciana

All of these additional species are found in the general region on prairie or in open places. The *Draba* usually prefers sand.

Four introduced species, which now occur quite rarely, should be added to these lists. *Trifolium pratense* is found in disturbed spots on both areas, and the following species still persist on the restored prairie:

Trifolium procumbens
Melilotus alba

Taraxacum erythrospermum

The invasion of the restored prairie strip took place almost entirely from the prairie side. There are probably two reasons for this: Most of these prairie species have their seeds distributed by wind, and the prevailing westerly and northwesterly winds of the summer and fall would bring seed mostly from the native prairie lying to the west; and the exposure of this open area to drying agencies would make it easier for the more xerophytic prairie flora to become established.

But for these circumstances the invasion might have taken place quite as readily from the contiguous forested tract on the east and north. The former lies on the upland and the latter along the bluffs,—both immediately adjacent to the restored tract.

It is interesting in this connection to note how entirely different the flora of these timbered tracts is from that of the nearby prairie. The following 24 species were found in both the upland woods and those of the banks and bluffs along Buffalo Slough in the vicinity of the restored prairie tracts:

Quercus macrocarpa
Quercus ellipsoidalis
Pyrus ioensis
Prunus serotina
Prunus virginiana
Psedera quinquefolia
Lonicera sempervirens
Botrychium virginianum

Smilax ecirrhata
Sanguinaria canadensis
Anemone virginiana
Desmodium grandiflorum
Geranium maculatum
Aralia nudicaulis
Thaspium aureum
Polemonium reptans

tions of the bluff area. It seems evident that the bluff area is the center of distribution for the more lasting woody plants, and that the upland forest has been produced by the gradual and limited advance of the forest flora under the protection of the plants of the forest border. This forest border here, as elsewhere in the state, is a fluctuating line or belt, which advances more or less during cycles of favorable seasons and retreats during the dry cycles. There is, however, no general advance or retreat.

The southern and western border of the upland woods is here formed by rather low, more or less scrubby oaks, *Q. ellipsoidalis* and *Q. macrocarpa*, and in its more open portions it frequently contains stray individuals or clumps of species which belong to the prairie of the region. The deeper woods, however, present a pure forest flora, which is also characteristic of the greater part of the sheltered bluffs belt which forms the northeastern part of this forest area, and which is itself limited by the swamp of Buffalo Slough.

Since the restored prairie is in direct contact with the forested area on the north and east sides it would not be surprising if the latter should invade it during some future cycle of moist seasons, but such advance would be a mere fluctuation such as has been noted. It is evident that in this case, with seemingly equal opportunities for the forest and prairie floras, the latter has taken possession of the restored tract to the exclusion of the former. When the prairie turf is once established it will probably hold its own against the encroachments of the forest if left undisturbed.

Conclusions

1.—It is evident that prairie areas may be restored after having been cultivated or otherwise disturbed. The prairie flora does not represent a transition state, but is a climax flora in its own right.

2.—The remnants of the prairie still persisting in the state are sufficient to furnish seed for the restoration of disturbed prairie areas, and this can be accomplished if the latter are simply left to themselves.

3.—The restoration of the prairie flora will occur gradually, the earlier transition stages representing various mixtures of floras determined by the character of the adjacent areas.

4.—An important part in this transformation is played by a certain group of native prairie plants, herein designated as prairie weeds, which quickly take possession of new surfaces. They form

the advance guard of the prairie flora, and have become weeds in cultivated areas.

5.—More recently certain introduced weeds assist the prairie weeds in this process of restoration.

6.—When the prairie is finally restored the prairie weeds may be incorporated in the renewed flora, probably usually in diminished numbers, but the introduced weeds practically disappear.

7.—It is evident that restoration of prairie tracts for incorporation with our state parks system here in Iowa is entirely feasible and can be accomplished at little additional expense.

8.—The views that prairie will disappear for all time if broken, and that with the cessation of prairie fires the forest will take possession of the prairie, are untenable in the light of the behavior of these and similar prairie tracts.

TABLE OF PRAIRIE PLANTS

The following table contains a list of all the plants found on the native prairie transects between Wilton and Summit, Iowa, and a corresponding partial record of the same (and a few additional) species for other areas indicated in the several columns by the letter x. The columns are numbered at the head as follows:

- I. Represents the native prairie south of Wilton, as noted.
- II. Includes the corresponding flora of the restored prairie in the same region.
- III. Includes the corresponding species of the roadbed in the same area.
- IV. Marks the corresponding species on the restored prairie at Mason City, Iowa.
- V. Contains the corresponding species on the restored prairie at Mason City.

Supplementary lists are given in the text in connection with the discussion of each of the localities.

Plants marked with an asterisk (*) have been introduced, but are sparingly established on the prairie.

Plants marked with an x before the name belong to the group herein designated as "prairie weeds."

The nomenclature of Gray's Manual, 7th edition, is employed for native or established plants, and that of Gray's School and Field Botany for other introduced plants. Hence authors' names are omitted throughout the paper.

PERSISTENCE OF THE PRAIRIE

21

TABLE OF PRAIRIE PLANTS

	I	II	III	IV	V
Family <i>Equisetaceae</i>					
x <i>Equisetum arvense</i>	+	+	+		
<i>Equisetum hyemale intermedium</i>	+	+	+		
Family <i>Gramineae</i>					
<i>Andropogon scoparius</i>	+	+	+	+	+
<i>Andropogon furcatus</i>	+	+	+	+	
<i>Sorghastrum nutans</i>	+	+	+	+	+
<i>Panicum virgatum</i>	+	+	+		
<i>Panicum huachucae</i>	+	+	+		
<i>Panicum Scribnerianum</i>	+	+	+	+	
<i>Stipa spartea</i>	+	+	+	+	
<i>Aristida basiramea</i>		+	+		
<i>Muhlenbergia racemosa</i>	+	+	+	+	+
* <i>Phleum pratense</i>		+	+	+	+
<i>Sporobolus heterolepis</i>	+		+	+	
<i>Agrostis hyemalis</i>	+	+	+		
<i>Agrostis alba vulgaris</i>	+		+	+	
<i>Sphenopholis obtusata</i>		+			
<i>Koeleria cristata</i>	+	+	+	+	
<i>Bouteloua curtipendula</i>	+			+	+
* <i>Poa compressa</i>	+	+	+	+	+
* <i>Poa pratensis</i>	+	+	+	+	+
x <i>Agropyron Smithii</i>	+		+	+	+
x <i>Hordeum jubatum</i>	+		+		+
<i>Elymus canadensis</i>	+	+	+	+	+
Family <i>Cyperaceae</i>					
<i>Cyperus filiculmis</i>	+	+	+		
<i>Carex scoparia</i>	+				
<i>Carex festuacea</i>	+	+	+	+	
<i>Carex grvida</i>			+		
<i>Carex pennsylvanica</i>	+	+			
Family <i>Commelinaceae</i>					
<i>Tradescantia reflexa</i>	+	+	+		
Family <i>Liliaceae</i>					
<i>Allium canadense</i>	+				
<i>Lilium philadelphicum</i>	+	+			
<i>Lilium philadelphicum andinum</i>	+				
* <i>Asparagus officinalis</i>	+	+	+		
<i>Smilacina stellata</i>	+		+	+	
Family <i>Amaryllidaceae</i>					
<i>Hypoxis hirsuta</i>	+				
Family <i>Iridaceae</i>					
<i>Sisyrinchium campestre</i>	+	+	+	+	
Family <i>Orchidaceae</i>					
<i>Spiranthes gracilis</i>	+			+	
Family <i>Salicaceae</i>					
<i>Salix humilis</i>	+	+	+	+	+
Family <i>Betulaceae</i>					
<i>Corylus americana</i>	+	+	+	+	
Family <i>Santalaceae</i>					
<i>Comandra umbellata</i>	+	+		+	
Family <i>Polygonaceae</i>					
<i>Rumex altissimus</i>	+	+	+		
<i>Polygonum ramosissimum</i>			+		
Family <i>Chenopodiaceae</i>					
<i>Chenopodium leptophyllum</i>		+			

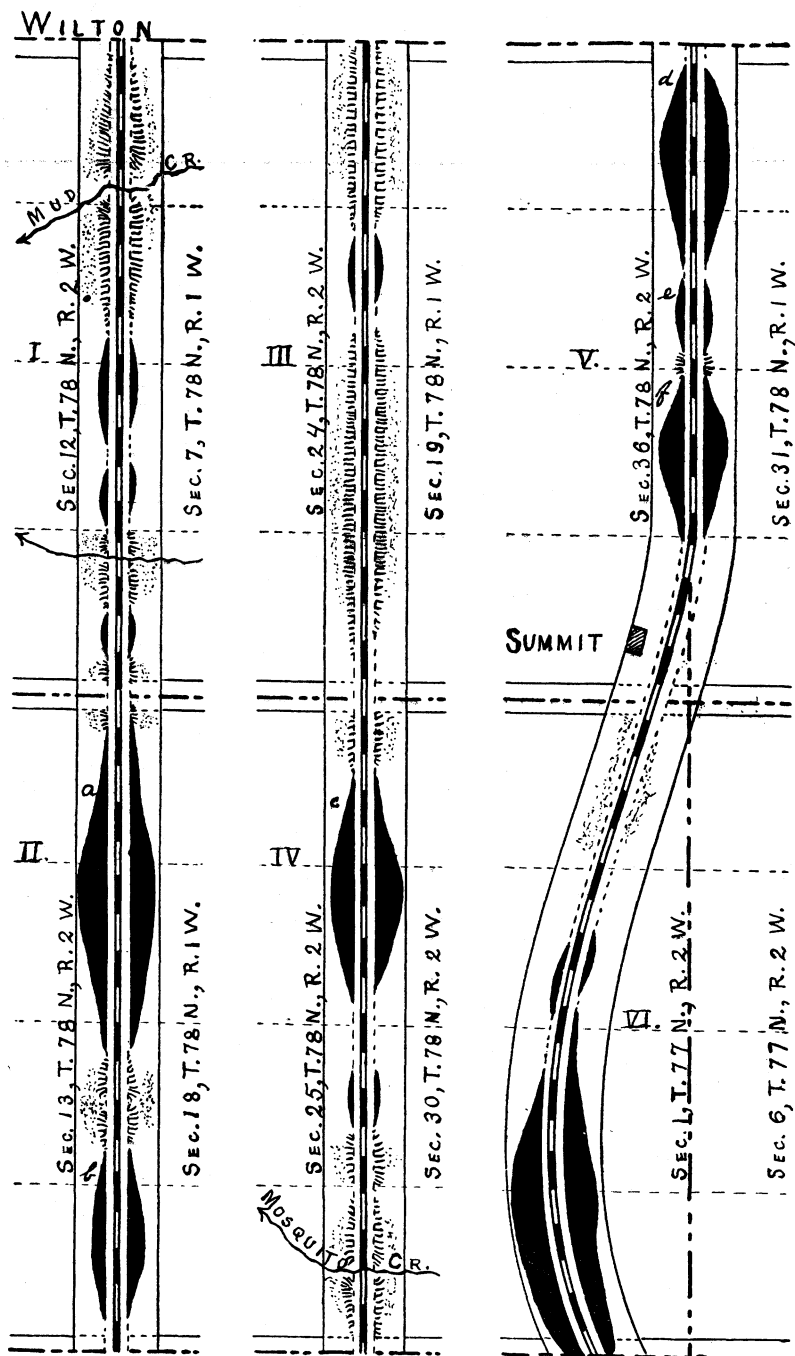
	I	II	III	IV	V
Family <i>Nyctaginaceae</i>					
x <i>Oxybaphus nyctagineus</i>	+		+		
Family <i>Caryophyllaceae</i>					
x <i>Silene antirrhina</i>	+		+	+	
<i>Silene stellata</i>	+			+	
Family <i>Ranunculaceae</i>					
<i>Ranunculus fascicularis</i>	+			+	+
<i>Thalictrum dasycarpum</i>	+			+	
<i>Anemone cylindrica</i>	+	+		+	+
<i>Anemone canadensis</i>	+		+		
Family <i>Cruciferae</i>					
x <i>Lepidium apetalum</i>	+	+	+	+	
Family <i>Saxifragaceae</i>					
<i>Heuchera hispida</i>	+	+	+	+	
Family <i>Rosaceae</i>					
<i>Spiraea salicifolia</i>	+	+	+		
<i>Fragaria virginiana</i>	+	+	+	+	+
<i>Potentilla arguta</i>	+	+	+	+	
x <i>Potentilla monspeliensis</i>			+	+	+
<i>Potentilla canadensis</i>	+	+	+		
<i>Rosa pratincola</i>	+	+	+	+	+
Family <i>Leguminosae</i>					
x <i>Cassia chamæcrista</i>	+	+	+		
<i>Baptisia bracteata</i>	+			+	
<i>Baptisia leucantha</i>	+				
<i>Amorpha canescens</i>	+	+	+	+	+
<i>Petalostemum purpureum</i>	+	+	+	+	+
<i>Petalostemum candidum</i>	+	+	+	+	+
<i>Astragalus canadensis</i>	+	+	+		
<i>Desmodium illinoense</i>	+	+	+		
<i>Desmodium canadense</i>	+	+	+	+	+
<i>Lespedeza capitata</i>	+	+	+	+	+
<i>Amphicarpa Pitcheri</i>	+	+	+	+	
x <i>Trifolium repens</i>		+	+	+	
Family <i>Linaceae</i>					
<i>Linum sulcatum</i>	+	+		+	+
Family <i>Oxalidaceae</i>					
<i>Oxalis violacea</i>	+		+	+	
x <i>Oxalis stricta</i>		+	+		
Family <i>Polygalaceae</i>					
<i>Polygala sanguinea</i>	+		+		
<i>Polygala Senega</i>	+		+	+	
<i>Polygala verticillata</i>	+				
Family <i>Euphorbiaceae</i>					
x <i>Euphorbia Preslii</i>			+		
<i>Euphorbia corollata</i>	+	+	+		
Family <i>Anacardiaceae</i>					
<i>Rhus glabra</i>	+	+	+	+	
Family <i>Rhamnaceae</i>					
<i>Ceanothus americanus</i>	+	+	+	+	+
Family <i>Vitaceae</i>					
<i>Vitis vulpina</i>	+	+	+	+	
Family <i>Hypericaceae</i>					
x <i>Hypericum cistifolium</i>	+		+		
Family <i>Cistaceae</i>					
<i>Helianthemum majus</i>	+		+		
<i>Helianthemum canadense</i>	+	+			
Family <i>Violaceae</i>					
x <i>Viola cucullata</i>		+	+		

PERSISTENCE OF THE PRAIRIE

23

	I	II	III	IV	V
<i>Viola fimbriatula</i>	+	+	+		
<i>Viola pedatifida</i>	+	+	+	+	+
Family <i>Onagraceae</i>					
x <i>Oenothera biennis</i>	+	+	+	+	
<i>Gaura biennis</i>		+	+	+	
Family <i>Umbelliferae</i>					
<i>Eryngium yuccifolium</i>	+	+	+	+	
<i>Zizia aurea</i>	+	+		+	
Family <i>Primulaceae</i>					
<i>Dodecatheon Meadia</i>	+				
Family <i>Gentianaceae</i>					
<i>Gentiana puberula</i>	+	+		+	
<i>Gentiana Andrewsii</i>	+				
<i>Gentiana flavida</i>	+	+		+	+
Family <i>Apocynaceae</i>					
x <i>Apocynum cannabinum</i>	+	+	+		
<i>Apocynum cannabinum hypericifolium</i>	+				
Family <i>Asclepiadaceae</i>					
<i>Asclepias tuberosa</i>	+	+	+	+	+
x <i>Asclepias syriaca</i>	+	+	+		
<i>Asclepias verticillata</i>	+	+	+		
<i>Acerates floridana</i>	+		+		
<i>Acerates viridiflora</i>	+	+	+		
<i>Acerates viridiflora lanceolata</i>	+	+		+	
Family <i>Convolvulaceae</i>					
x <i>Convolvulus sepium</i>	+	+	+		
Family <i>Polemoniaceae</i>					
<i>Phlox pilosa</i>	+	+	+	+	+
Family <i>Hydrophyllaceae</i>					
x <i>Ellisia nyctelea</i>	+		+		
Family <i>Boraginaceae</i>					
<i>Lithospermum canescens</i>	+	+	+	+	
Family <i>Verbenaceae</i>					
x <i>Verbena stricta</i>	+	+	+		
Family <i>Labiatae</i>					
<i>Scutellaria parvula</i>		+	+		
<i>Monarda mollis</i>	+	+	+	+	+
x <i>Hedeoma hispida</i>		+	+	+	+
<i>Pycnanthemum flexuosum</i>	+	+	+		
<i>Pycnanthemum pilosum</i>	+	+			
Family <i>Solanaceae</i>					
x <i>Physalis pruinosa</i>	+		+	+	
<i>Physalis virginiana</i>	+	+	+	+	
Family <i>Scrophulariaceae</i>					
<i>Scrophularia leporella</i>	+		+	+	
<i>Veronica virginica</i>	+	+	+		
<i>Gerardia auriculata</i>	+				
<i>Gerardia aspera</i>	+				
<i>Gerardia purpurea</i>	+				
<i>Gerardia Skinneriana</i>	+				
<i>Pedicularis canadensis</i>	+	+		+	
Family <i>Acanthaceae</i>					
<i>Ruellia ciliosa</i>			+		
Family <i>Campanulaceae</i>					
x <i>Specularia perfoliata</i>		+	+		
Family <i>Lobeliaceae</i>					
<i>Lobelia spicata</i>	+	+	+	+	+

	I	II	III	IV	V
Family <i>Compositae</i>					
Kuhnia eupatoroides corymbulosa	+	+	+	+	
Liatris cylindracea	+				
Liatris scariosa	+	+		+	+
Liatris pycnostachya	+	+	+		
Solidago speciosa angustata	+	+	+	+	+
Solidago missouriensis	+	+	+		
Solidago nemoralis	+	+	+	+	+
Solidago canadensis	+	+	+	+	+
xSolidago rigida	+	+	+	+	+
Solidago graminifolia	+	+	+		
Aster novæ-angliæ	+		+	+	
Aster sericeus	+	+		+	
Aster azureus	+	+	+	+	+
Aster lævis	+	+	+	+	+
Aster multiflorus	+	+	+	+	+
Aster paniculatus	+	+	+		
xErigeron ramosus	+	+	+	+	+
xErigeron canadensis	+	+	+	+	
Antennaria neglecta	+	+	+	+	
Silphium laciniatum	+	+	+		
Silphium integrifolium	+	+	+		
Parthenium integrifolium	+	+	+		
xAmbrosia trifida	+	+	+		
xAmbrosia artemisiifolia		+	+	+	
xAmbrosia psilostachya	+	+	+	+	
Heliopsis scabra	+	+	+	+	+
Rudbeckia subtomentosa	+				
Rudbeckia hirta	+	+	+	+	+
Brauneria pallida	+	+	+		
Lepachys pinnata	+	+	+	+	+
Helianthus scaberrimus	+	+	+	+	+
Helianthus occidentalis	+	+	+	+	
xHelianthus grosseserratus	+	+	+	+	
Helianthus tuberosus	+		+		
Coreopsis palmata	+	+	+	+	+
Coreopsis tripteris	+	+	+		
xAchillea millefolium	+	+	+	+	+
Artemisia caudata	+	+		+	+
Artemisia serrata	+				
Artemisia ludoviciana	+	+	+	+	+
Cacalia tuberosa	+				
Senecio plattensis	+		+	+	+
Cirsium discolor	+	+	+	+	+
Cirsium iowense	+				
Cirsium Hillii	+	+		+	
Krigia amplexicaulis	+				
Lactuca canadensis	+	+	+	+	
Prenanthes racemosa	+	+	+		



Wilton-Summit tract
(For explanation see next page)



EXPLANATION OF PLAT OF WILTON-SUMMIT TRACT

Each of the three sections represents 2 miles.

Miles are numbered from north to south with Roman numerals.

The horizontal dotted lines mark quarter miles.

The section lines are marked with heavy broken lines.

The railway runs on section lines to near Summit.

Its right of way and the intersecting roads are marked with full lines. Both are exaggerated in width.

The cross-lines mark the fills, the largest about 9 feet high.

The dotted areas are low and wet.

The black areas represent cuts. They are distributed as follows:

Mile I.—Three cuts 3 to 5 feet deep.

Mile II.—Cut a is about one-half mile long and reaches 11 feet in depth.

Cut b is about 100 yards long and 8 feet deep.

Mile III.—One cut 3 feet deep.

Mile IV.—Cut c, more than 450 yards long and reaching 14 feet in depth.

Mile V.—Cut d, nearly 500 yards long and 14 feet deep.

Cut e, less than 200 yards long and 5 feet deep.

Cut f, about 180 yards long and 8 feet deep.

Mile VI.—The large cut is just outside of our area.

PLATE II

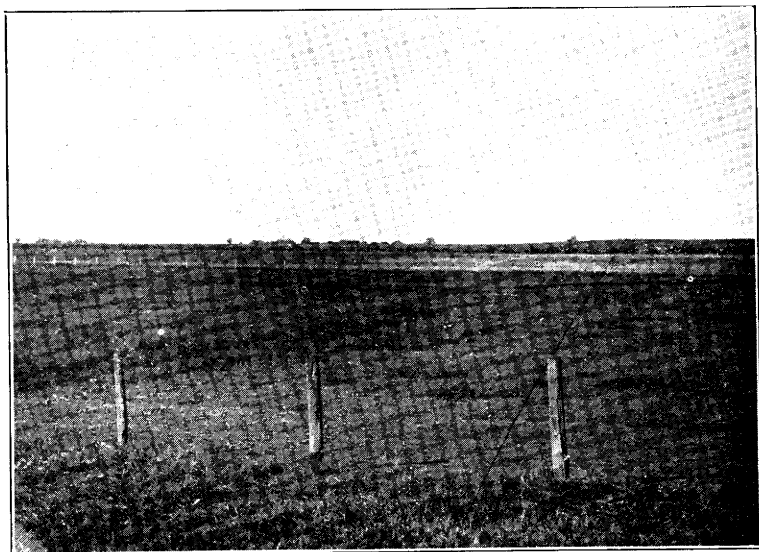


Fig. 1. Illinoian drift prairie south of Wilton.

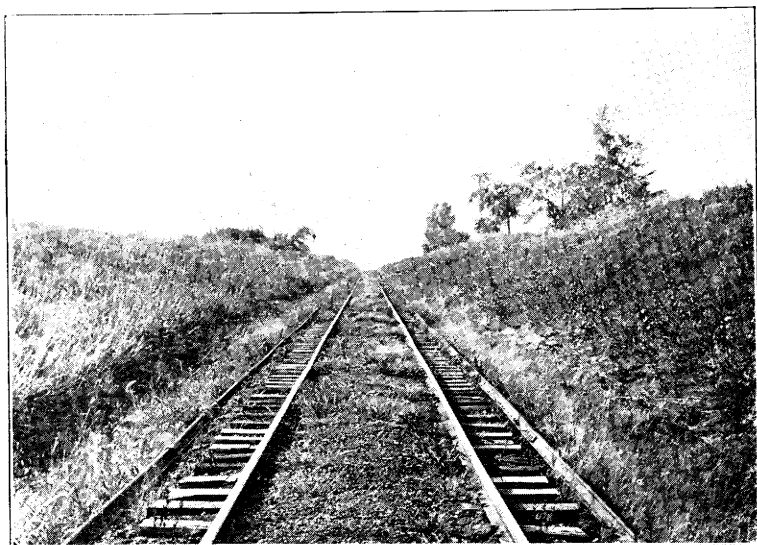


Fig. 2. Cut a, looking south. Shows restored prairie. South of Wilton.

PLATE III

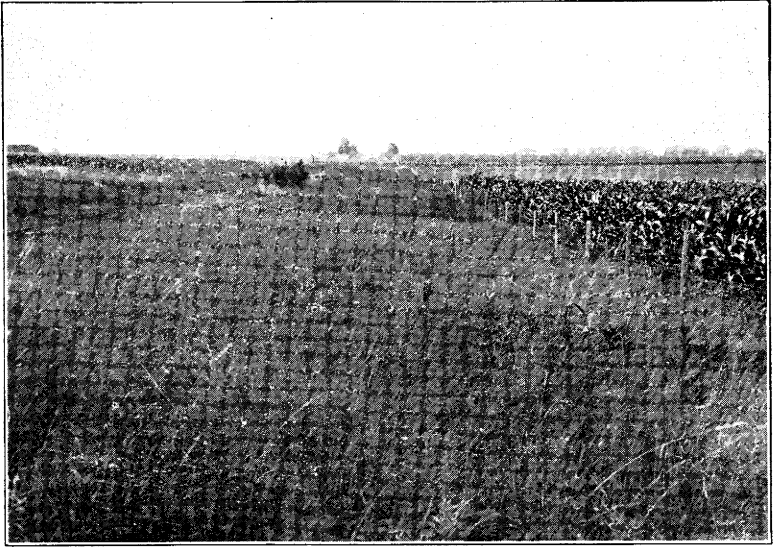


Fig. 1. Native prairie along railway. Looking north from cut b.
Partly low. South of Wilton.



Fig. 2. Native prairie at cut a. Looking south.

PLATE IV

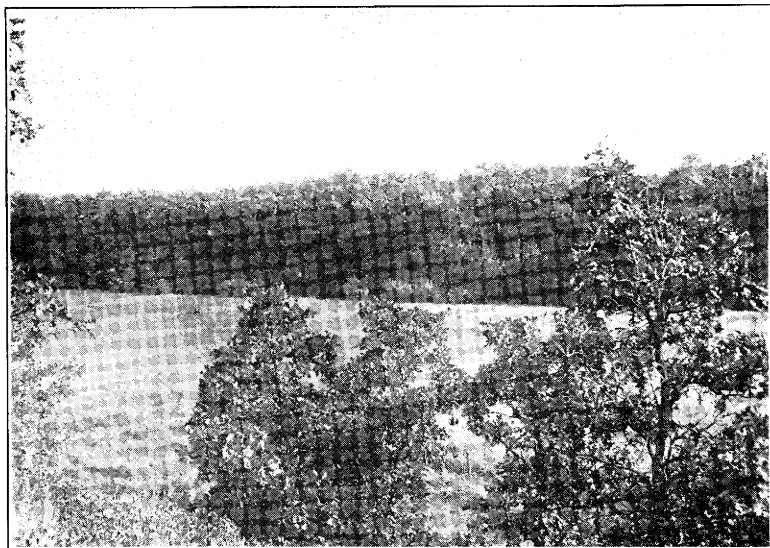


Fig. 1. Looking nearly south across Buffalo Slough towards the wooded bluffs just east of restored prairie. Mason City.



Fig. 2. A bit of native prairie with forest border. Near restored prairie at Mason City.



THE PRAIRIE FLORA OF MANITOBA

B. SHIMEK

The prairies originally occupied a large part of the Mississippi Valley and the region to the north. They extended southward to Oklahoma and Texas; eastward through Illinois, Indiana and Ohio, including also the barrens of Kentucky and Tennessee; and westward and northwestward, including seven-eighths of the area of Iowa, the southern and western parts of Minnesota, eastern Kansas, Nebraska and the Dakotas, and thence into the southern portions of the provinces of Canada east of the Rocky Mountains.

They extended over almost every type of topography and soil found within that area, and there is nothing in either which definitely marks or determines the character of the prairie. There is substantial agreement in but one character,—the flora. The prairies are treeless, or practically so, and the greater part of the flora consists of perennial herbs of a distinctly xerophytic type, the Gramineæ being most numerous in individuals though exceeded by the Compositæ in number of species, with the Leguminosæ following as third in order.

The prairies were continuous over large areas, or were interrupted by groves, swamps and sand-dune areas, or were limited to small areas hemmed in by forest or swamp. Whatever their extent, however, they agreed in the character of their original flora, now reduced over most of the area to mere remnants. The typical prairie flora, as represented in Iowa, extended over the entire area, but at its western margins it blended more or less with the still more xerophytic flora of the great plains.

The present paper presents a brief discussion of this flora as it appears in a portion of southern Manitoba, still well within the prairie area, but near its northern border. The vicinity of Carberry, about 100 miles west of Winnipeg, was chosen for study because an earlier list of the flora of the region had been published by Christy.¹ This list was prepared on the basis of observations made in 1883 and 1884, when the region was just being settled and

¹Christy, R. Miller, Notes on the Botany of Manitoba. Journal of Botany, vol. XXV, 1887.

presented much of the prairie in its primitive condition. In 1920 the writer found the prairie of the region mostly under cultivation, but few tracts remaining unbroken. The best illustrations of the prairie flora were preserved in the unbroken strips along the railway right of way, and on limited tracts west and northwest of Carberry. For an illustration of the latter see Plate VI, fig. 1.

The Canadian Pacific Railway was constructed when the region was still practically unsettled, and its right of way has preserved a transect of the native prairie along both sides of the roadbed for about three miles on either side of Carberry. A portion of it is illustrated in Plate VI, fig. 2. The Canadian Northern Railway has little prairie on its right of way north and south of the station as it was built after most of the surface was broken. Some attention was also given to the strips of prairie along the Canadian Pacific right of way both east and west of MacGregor,—about thirty miles east of Carberry.

Carberry lies in a lobe of the prairie plain which is bounded by the northern margin of the great sand-dune area which extends along the Assiniboine River for about 150 miles. The location of the lobe is shown in the map, Plate V. Its surface is quite level, being somewhat broken only by a few very shallow kettleholes (now mostly dry), and near the margins by low outliers of the dune area. Its marginal portions and irregular areas scattered over its surface are quite sandy, but most of it is fertile and was originally covered with a prairie flora, which was interrupted only by the kettleholes. The latter were bordered by a marsh flora, of which little remains, in some cases, and by thickets consisting largely of *Populus tremuloides*, some of which still persist.

The sand-dune area, which extends for many miles along the southern border of the prairie of which the Carberry lobe is a part, was studied only in the region including the lobe. Much of its border is quite abrupt, but occasionally it shades off gradually into sandy prairie, as at Brandon Junction. Its surface presents a variety of features. Much of it is of the usual dune type (see Plate VIII, fig. 2), but there are large gently sloping or flat areas, which, though very sandy, are largely covered with a prairie flora. Such areas are shown in Plate VII, fig. 2, and Plate VIII, fig. 1.

One of the finest areas of this type is known as Spruce Plain. It is located southwest of Carberry, and a little of the eastern mar-

gin is shown on the map, Plate V. It lies in the heart of the dune area, but its surface is flat, or but gently rolling. A portion of it is shown in Plate VII, fig. 2. While a large part of it is treeless, thickets and clumps of white spruce, *Picea canadensis*, are scattered over its surface, giving it its name. The treeless surfaces are covered with an almost pure prairie flora.

The rougher portions of the dune area are more or less covered with thickets, particularly in the depressions and around the ponds or bogs which occupy them. The largest of these swamps lies a little to the west of the area mapped, and is an extensive tamarack muskeg which surrounds a small lake.

The dune area crosses the Canadian Pacific about four miles west of Carberry, and a narrow lobe extends northward about three miles to the east, as shown on the map. Another lobe crosses the line of the railway near Sidney, east of the area mapped; but beyond that, eastward, the border of the sandhills sweeps well to the south.

The MacGregor area is typical, nearly level fertile prairie, and practically all excepting the right of way is under cultivation. The latter shows good transects of native prairie, varied occasionally by slight depressions which contain a marsh flora. Some of the depressions in this region are also bordered by thickets.

THE FLORA

No detailed study of the flora of the swamp areas and thickets was attempted, but incidental observations were made in connection with the closer study of the xerophytic flora of the prairies and the dunes. Some notes on these observations will be of interest because they reveal the floral types which occupy modified portions of these xerophytic areas.

The Swamp Flora.—The finest display of this flora was presented by the great muskeg in the Spruce Plain region. The following list of plants will suggest the general floral character of the area, the tamarack being dominant over its greater part:

<i>Larix laricina</i>	<i>Salix candida</i>
<i>Equisetum fluviatile</i>	<i>Salix petiolaris</i>
<i>Triglochin maritima</i>	<i>Sarracenia purpurea</i>
<i>Calamagrostis canadensis</i>	<i>Parnassia palustris</i>
<i>Eriophorum angustifolium majus</i>	<i>Menyanthes trifoliata</i>
<i>Carex hystrixina</i>	<i>Galium Claytoni</i>
<i>Tofieldia glutinosa</i>	<i>Lobelia Kalmii</i>
<i>Smilacina trifolia</i>	<i>Aster junceus</i>
<i>Habenaria hyperborea</i>	

In the smaller more or less marshy tracts on the prairie and dune areas the following additional species were observed:

<i>Equisetum hyemale robustum</i>	<i>Caltha palustris</i>
<i>Typha latifolia</i>	<i>Ribes floridum</i>
<i>Alisma plantago-aquatica</i>	* <i>Spiræa salicifolia</i>
<i>Phalaris arundinacea</i>	<i>Potentilla fruticosa</i>
* <i>Agrostis alba</i>	<i>Rubus triflorus</i>
<i>Calamovilfa longifolia</i>	<i>Lathyrus palustris</i>
<i>Spartina Michauxiana</i>	<i>Lathyrus palustris myrtifolius</i>
<i>Spartina gracilis</i>	* <i>Epilobium angustifolium</i>
<i>Phragmites communis</i>	<i>Hippuris vulgaris</i>
<i>Eragrostis Frankii</i>	<i>Cicuta maculata</i>
<i>Poa triflora</i>	<i>Sium cicutæfolium</i>
<i>Elymus virginicus</i>	<i>Cornus stolonifera</i>
<i>Scirpus validus</i>	<i>Steironema ciliatum</i>
<i>Eriophorum angustifolium majus</i>	<i>Apocynum cannabinum</i>
<i>Carex filiformis</i>	<i>hypericifolium</i>
<i>Carex Sartwellii</i>	<i>Gentiana Andrewsii</i>
<i>Carex Bebbii</i>	<i>Asclepias incarnata</i>
<i>Spirodela polyrhiza</i>	* <i>Stachys palustris</i>
<i>Juncus bufonius</i>	<i>Mentha arvensis canadensis</i>
<i>Juncus balticus littoralis</i>	<i>Castilleja pallida septentrionalis</i>
<i>Lilium canadense</i>	<i>Pedicularis lanceolata</i>
<i>Cypripedium parviflorum</i>	<i>Plantago eriopoda</i>
<i>Salix longifolia</i>	<i>Campanula aparinoides</i>
<i>Salix discolor</i>	<i>Aster umbellatus</i>
* <i>Salix rostrata</i>	<i>Erigeron philadelphicus</i>
<i>Betula pumila glandulifera</i>	<i>Artemisia biennis</i>
<i>Urtica gracilis</i>	<i>Petasites sagittatus</i>
<i>Rumex mexicanus</i>	<i>Cirsium muticum</i>
* <i>Anemone canadensis</i>	

Several of the species in this list also appear in the prairie list. They are marked with an asterisk. These species usually grow in moist places, but sometimes they extend to drier prairies. *Ribes floridum* also appears in moist woods.

The Forest Flora.—Two groups of forest plants are more or less distinguishable in this region,—those of the more xerophytic dunes, and those of the sheltered ravines and borders of swamps or ponds.

The following list includes the species observed on the dry dunes, —often in thickets:

<i>Picea canadensis</i>	<i>Amelanchier spicata</i>
<i>Bromus ciliatus</i>	<i>Cratægus</i> , sp.
* <i>Bromus purgans</i>	<i>Agrimonia striata</i>
<i>Smilax herbacea pulverulenta</i>	<i>Prunus virginiana</i>
<i>Populus tremuloides</i>	<i>Prunus pennsylvanica</i>
* <i>Quercus macrocarpa</i>	* <i>Rhus Toxicodendron</i>
<i>Thalictrum dioicum</i>	* <i>Elæagnus argentea</i>
<i>Actæa rubra</i>	<i>Monarda fistulosa</i>
<i>Arabis canadensis</i>	<i>Lonicera glaucescens</i>

The species marked with an asterisk are also found in the prairie list.

The following species are usually found near the borders of thickets, and may extend out on the prairie:

Bromus ciliatus	Prunus virginianus
Smilax herbacea pulverulenta	Rubus idæus
*Corylus americana	Rubus occidentalis
Polygonum scandens	Sanicula marilandica
Erysimum cheiranthoides	

The *Corylus* is also frequent on the prairie, and the species of *Prunus* and *Rubus* have probably been carried out upon the prairie by birds, as they are usually found along fences or telegraph wires, which serve as perches for birds.

The following species were found in the more moist and better sheltered thicket:

Equisetum pratense	Thaspium aureum
Equisetum sylvaticum	Cornus canadensis
Agrostis perennans	Pyrola elliptica
Populus balsamifera	Pyrola americana
Populus acuminata	*Steironema ciliatum
Betula alba	Castilleja miniata
Alnus incana	Viburnum opulus americanum
Anemone virginiana	Eupatorium purpureum
Actæa alba	Solidago ulmifolia
Ribes floridum	*Solidago serotina
Rubus triflorus	Rudbeckia laciniata
Rosa blanda	Cacalia suaveolens
Acer Negundo	Lactuca spicata
*Epilobium angustifolium	Prenanthes alba
Aralia nudicaulis	

The species marked with an asterisk also appear upon richer prairie.

A few prairie plants may also be found in the more open portions of the groves. The following were noted:

Equisetum hyemale intermedium	Convolvulus sepium
Elymus canadensis	Agastache Fœniculum
Thalietrum dasycarpum	Galium boreale
Heuchera hispida	Symphoricarpos occidentalis
Fragaria virginiana	Rudbeckia hirta

The Dune Flora.—The Manitoba prairie list shows 96 species of prairie plants which are also found upon the dunes bordering the Carberry prairie lobe. They were collected east, west and south of Carberry. In addition to these prairie species the dunes and sandy areas yielded the following distinctively sand species:

Selaginella rupestris	Androsace occidentalis
Juniperus horizontalis	Opuntia polyacantha
Cyperus Schweinitzii	Arctostaphylos Uva-ursi
Chamaerhodos erecta	

Geum triflorum and *Asclepias tuberosa* were also found here only on the dunes, but both occur on ordinary prairie elsewhere. *Arabis*

Drummondii, which is given in the prairie list, was also found here only upon sandy areas. It is scarcely a characteristic prairie plant, but occurs on dry areas of various types. *Panicum Scribnerianum* is likewise found on ordinary prairie elsewhere.

The Prairie Flora.—The prairie flora may be considered in two rather illy-defined groups. The one includes the plants of the sandy prairie collected within the Carberry lobe, and the other the flora of the more fertile prairie.

The former is listed in column II, of the Manitoba prairie list, and its 125 species differ from those of the richer prairie only in that the less xerophytic forms are wanting, and that two species of sand plants are included, namely *Androsace occidentalis* and *Arctostaphylos Uva-ursi*. *Polygala Senega* and *Acerates viridiflora* were collected only upon the sandy prairie, but they occur on ordinary prairie almost everywhere.

The flora of the more fertile prairie in the vicinity of Carberry is listed in column I, and that from the prairie at MacGregor in column IV. It will be observed that the more fertile prairie of MacGregor yielded several species, belonging to the genera *Sorghastrum*, *Panicum*, *Sporobolus*, *Sisyrinchium*, *Amorpha*, *Asclepias*, *Helianthus* and *Prenanthes*, which are characteristic of the richer prairies in Iowa, and elsewhere, but which are lacking on the Carberry prairie. The latter, however, yielded 130 species, as against 110 from MacGregor. The additional species from Carberry are mostly more xerophytic types. The locality was more thoroughly worked than that at MacGregor, and that may account in part for the difference.

The 15 species marked with an asterisk in the Manitoba prairie list, are not known on the prairies of Iowa. Several are far western and northwestern species, and a few like the species of *Lychnis* and *Erysimum*, are scarcely characteristic prairie plants, but may occur in almost any dry situation. The great bulk of this prairie flora is identical with that of Iowa.

Column V contains the species reported by Christy,—in some cases under other names than those here employed. He does not report *Anemone cylindrica*, but evidently included it with *A. virginiana*, both being very common. Two evident errors occur in the report of *Quercus alba* and *Juniperus virginiana* from the sand-hills. The former is undoubtedly *Q. macrocarpa*, which is very common, and the latter is *Juniperus horizontalis*.

Several of the species in his list were not found by the writer, but among them only the following are prairie or sand species:

<i>Helianthemum canadense</i>	<i>Astragalus monticola</i>
<i>Geranium carolinianum</i>	<i>Aster vimineus</i>
<i>Astragalus caryocarpus</i>	<i>Castilleja coccinea</i>

Christy's explanation of the cause of the treelessness of the prairies (fire) will be discussed by the writer elsewhere.

The Weed Flora.—It is interesting to compare Christy's list of weeds with those collected by the writer thirty-six years later. The country was comparatively new when his observations were made, and the list is short; it may be incomplete even for that date. The entrance of railways into this territory, however, and the general settlement and cultivation of the country, no doubt greatly increased the number of introduced weeds. Some of the native prairie plants given in the Manitoba list have also become weeds. They are discussed as "prairie weeds" in the preceding article.

The following species of introduced weeds were found chiefly along the roadbeds of the railways at Carberry and MacGregor. With them were associated various native prairie plants but mostly in small numbers. Few enter the prairie transect in the right of way, excepting where the surface has been disturbed. The list follows:

<i>Setaria viridis</i>	<i>Sisymbrium altissimum</i>
<i>Phleum pratense</i>	<i>Capsella bursa-pastoris</i>
<i>Avena fatua</i>	<i>Trifolium pratense</i>
<i>Bromus secalinus</i>	<i>Trifolium hybridum</i>
<i>Lolium multiflorum</i>	<i>Melilotus alba</i>
<i>Polygonum aviculare</i>	<i>Melilotus officinalis</i>
<i>Polygonum convolvulus</i>	<i>Lathyrus pratensis</i>
* <i>Chenopodium album</i>	<i>Linum usitatissimum</i>
* <i>Chenopodium Bonus-Henricus</i>	<i>Lappula echinata</i>
<i>Salsola Kali</i>	<i>Plantago major</i>
<i>tenuifolia</i>	<i>Plantago lanceolata</i>
<i>Amaranthus retroflexus</i>	<i>Helianthus annuus</i>
<i>Silene noctiflora</i>	<i>Tanacetum vulgare</i>
* <i>Saponaria Vaccaria</i>	<i>Artemisia Absinthium</i>
<i>Portulaca oleracea</i>	<i>Cirsium arvense</i>
<i>Thlaspi arvense</i>	<i>Taraxacum officinale</i>
<i>Lepidium virginicum</i>	<i>Taraxacum erythrospermum</i>
<i>Brassica arvensis</i>	<i>Sonchus arvensis</i>
<i>Conringia orientalis</i>	<i>Crepis tectorum</i>

Those marked with an asterisk were reported also by Christy. He added *Lychnis githago*, which the writer did not find.

While these weeds have freely invaded the roadbed and the cultivated fields on either side, they are excluded by the unbroken prairie turf here as elsewhere. Associated with these weeds on the

roadbed were the following species which were evidently introduced from some other part of the country, or from the United States:

Poa pratensis

Polanisia trachysperma

Potentilla Anserina

They also fail to enter the unbroken prairie.

The prairie flora of Manitoba is very similar to that of Iowa in identity of species, and it is quite as persistent.

TABLE OF THE PRAIRIE FLORA

The following list includes the Manitoba prairie plants which were found by the writer, and those which occur on the sandy areas are also noted.

Column I includes those from fertile prairie in or near Carberry.

Column II includes those from sandy prairie near Carberry.

Column III includes those from the treeless dune areas around the Carberry lobe.

Column IV includes those from the fertile prairie near MacGregor.

Column V includes the prairie species also reported by Christy.

Those marked with an asterisk (*) are not known from the prairies of Iowa.

The nomenclature of Gray's Manual is used in this paper excepting in the case of the few species not included in that work. In such cases Britton's Manual is followed.

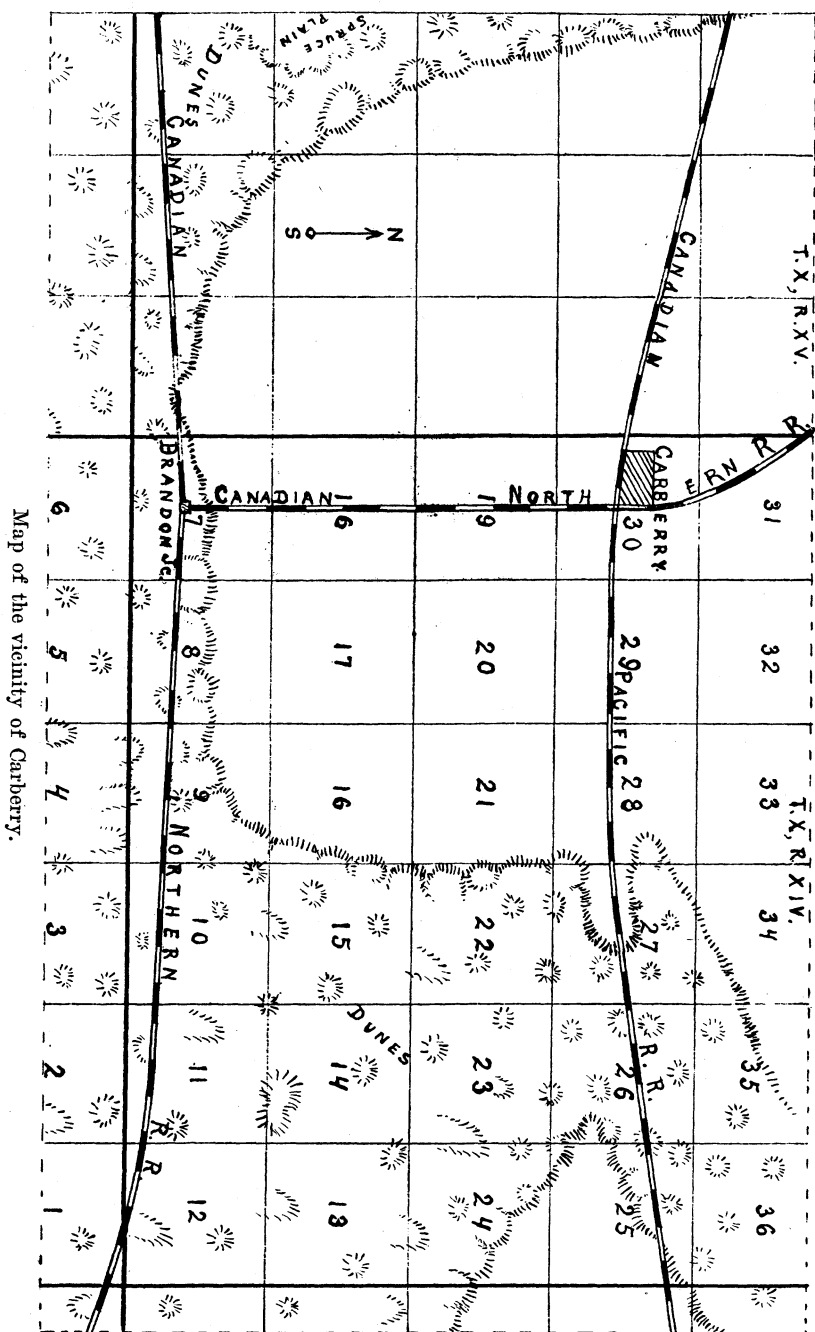
	I	II	III	IV	V
Family <i>Equisetaceae</i>					
<i>Equisetum arvense</i>	+	+		+	
<i>Equisetum hyemale intermedium</i>	+	+	+	+	
Family <i>Gramineae</i>					
<i>Andropogon scoparius</i>	+	+	+	+	
<i>Andropogon furcatus</i>	+	+	+	+	+
<i>Sorghastrum nutans</i>				+	
<i>Panicum Scribnerianum</i>		+	+		
<i>Panicum virgatum</i>				+	
* <i>Stipa viridula</i>	+	+	+		
<i>Stipa comata</i>	+				+
<i>Stipa spartea</i>	+	+	+	+	+
<i>Aristida basiramea</i>		+	+	+	
<i>Muhlenbergia racemosa</i>	+	+	+	+	
<i>Sporobolus cryptandrus</i>	+	+	+	+	
<i>Sporobolus heterolepis</i>				+	
<i>Sporobolus brevifolius</i>		+		+	
<i>Agrostis alba</i>	+				
<i>Agrostis hyemalis</i>	+	+	+	+	
<i>Koeleria cristata</i>	+	+	+	+	
<i>Bouteloua oligostachya</i>	+	+	+		
<i>Bouteloua hirsuta</i>		+			
<i>Bouteloua curtipendula</i>		+	+		
<i>Poa compressa</i>	+	+		+	

	I	II	III	IV	V
<i>Festuca octoflora</i>	+		+		
<i>Bromus purgans</i>	+	+	+		
<i>Agropyron Smithii</i>	+	+		+	
<i>Agropyron tenerum</i>	+				
<i>Agropyron caninum</i>	+				
<i>Agropyron Richardsonii</i>	+	+	+	+	
<i>Hordeum jubatum</i>	+	+			
<i>Elymus canadensis</i>	+	+	+	+	
Family <i>Cyperaceae</i>					
<i>Carex straminea</i>	+				
Family <i>Liliaceae</i>					
<i>Zygadenus chloranthus</i>	+	+		+	+
<i>Allium stellatum</i>	+	+	+	+	+
<i>Lilium philadelphicum</i>			+	+	+
<i>Smilacina stellata</i>		+	+	+	
Family <i>Iridaceae</i>					
<i>Sisyrinchium campestre</i>				+	+
Family <i>Salicaceae</i>					
<i>Salix humilis</i>	+	+	+		
<i>Salix rostrata</i>	+	+		+	
Family <i>Fagaceae</i>					
<i>Corylus americana</i>	+	+	+		
<i>Quercus macrocarpa</i>	+	+	+		
Family <i>Santalaceae</i>					
<i>Comandra umbellata</i>	+		+		
<i>Comandra pallida</i>	+	+	+		
Family <i>Amaranthaceae</i>					
<i>Amaranthus blitoides</i>	+	+			
Family <i>Nyctaginaceae</i>					
<i>Oxybaphus hirsutus</i>	+	+	+	+	
Family <i>Caryophyllaceae</i>					
<i>Arenaria stricta</i>	+	+			
<i>Cerastium arvense</i>	+	+	+	+	
* <i>Lychnis Drummondii</i>	+				
Family <i>Ranunculaceae</i>					
* <i>Thalictrum confine</i>	+	+	+	+	
<i>Thalictrum dasycarpum</i>		+		+	
<i>Anemone patens Wolfgangiana</i>	+	+	+	+	
<i>Anemone cylindrica</i>	+	+	+	+	
<i>Anemone canadensis</i>	+	+		+	
Family <i>Cruciferae</i>					
<i>Lepidium apetalum</i>	+	+	+	+	
<i>Sisymbrium canescens</i>	+			+	
<i>Sisymbrium canescens brachycarpon</i>	+	+	+	+	
<i>Arabis Drummondii</i>		+	+		
<i>Arabis lyrata</i>		+	+	+	
<i>Arabis glabra</i>		+			
* <i>Erysimum parviflorum</i>		+		+	
* <i>Erysimum asperum</i>	+	+	+		
Family <i>Capparidaceae</i>					
<i>Cleome serrulata</i>	+			+	
Family <i>Saxifragaceae</i>					
<i>Heuchera hispida</i>	+	+	+	+	+
Family <i>Rosaceae</i>					
<i>Spiraea salicifolia</i>	+	+	+	+	+
<i>Fragaria virginiana</i>	+	+	+	+	
<i>Potentilla arguta</i>	+	+	+	+	
<i>Potentilla monspeliensis</i>	+	+		+	+

	I	II	III	IV	V
Potentilla pennsylvanica	+	+	+		
*Potentilla Hippeana	+	+	+		
Rosa acicularis	+	+	+	+	+
Rosa pratincola	+	+	+	+	
Prunus pumila	+	+	+		
*Prunus Besseyi	+				
Family <i>Leguminosae</i>					
Trifolium repens	+				
Psoralea argophylla	+	+		+	+
Psoralea esculenta	+		+		+
Amorpha canescens				+	
Petalostemum purpureum	+	+	+	+	+
Petalostemum candidum	+	+	+	+	+
Astragalus canadensis	+	+		+	+
*Astragalus adsurgens	+	+	+	+	+
Oxytropis Lambertii	+		+		+
*Oxytropis splendens				+	
Glycyrrhiza lepidota	+	+		+	+
Vicia americana	+	+		+	+
Vicia americana linearis	+	+		+	+
Lathyrus venosus	+	+	+	+	+
Family <i>Linaceae</i>					
Linum rigidum	+				
Linum sulcatum	+		+		+
Family <i>Polygalaceae</i>					
Polygala Senega		+			+
Family <i>Euphorbiaceae</i>					
Euphorbia serpyllifolia	+	+		+	
Family <i>Anacardiaceae</i>					
Rhus Toxicodendron	+	+	+	+	
Family <i>Violaceae</i>					
Viola pedatifida	+	+	+		
Family <i>Elaeagnaceae</i>					
*Elaeagnus argentea	+	+	+	+	+
Family <i>Onagraceae</i>					
Epilobium angustifolium	+	+			
Oenothera muricata	+	+			
Oenothera biennis	+	+	+	+	+
*Oenothera pallida	+	+	+		
Oenothera serrulata	+	+			+
Gaura coccinea	+	+			
Family <i>Umbelliferae</i>					
Zizia aurea	+	+	+	+	
Zizia cordata	+	+	+	+	
Family <i>Apocynaceae</i>					
Apocynum cannabinum			+	+	
Family <i>Asclepiadaceae</i>					
Asclepias speciosa				+	
Asclepias ovalifolia	+				
Acerates viridiflora		+			
Family <i>Convolvulaceae</i>					
Convolvulus sepium	+			+	
Family <i>Boraginaceae</i>					
Lappula Redowskii occidentalis	+	+		+	
Lithospermum canescens	+	+	+	+	+
Lithospermum angustifolium		+	+		
Family <i>Labiatae</i>					
Teucrium canadense				+	

	I	II	III	IV	V
Agastache Fœniculum	+	+	+	+	+
Dracocephalum parviflorum	+	+			
Stachys palustris		+		+	
Monarda mollis	+	+	+	+	+
Family <i>Solanaceae</i>					
Physalis virginiana	+	+	+	+	
Family <i>Scrophulariaceae</i>					
Pentstemon gracilis	+	+	+	+	
*Orthocarpus luteus	+	+		+	+
Pedicularis canadensis				+	+
Family <i>Rubiaceae</i>					
Galium boreale	+	+	+	+	+
Houstonia longifolia	+	+			
Family <i>Caprifoliaceae</i>					
Symphoricarpos occidentalis	+	+		+	+
Symphoricarpos racemosus parviflorus	+				
Family <i>Campanulaceae</i>					
Campanula rotundifolia	+	+	+	+	+
Family <i>Lobeliaceae</i>					
Lobelia spicata		+		+	
Family <i>Compositae</i>					
Liatris punctata	+	+	+		+
Liatris scariosa	+	+	+	+	+
Chrysopsis villosa	+	+	+	+	+
Solidago missouriensis	+	+	+	+	
Solidago nemoralis	+	+	+	+	
Solidago canadensis gilvocanescens	+	+	+	+	
Solidago serotina		+	+	+	
Solidago rigida	+	+	+	+	+
Solidago graminifolia	+	+	+	+	
Aster novæ-angliæ		+	+	+	+
Aster lævis	+	+	+	+	+
Aster multiflorus	+	+	+	+	
Aster ptarmicoides	+	+	+	+	+
*Erigeron glabellus	+	+	+	+	+
Erigeron ramosus		+	+	+	
Erigeron canadensis	+	+	+	+	
Antennaria neodioica			+	+	
Antennaria neglecta			+		
Iva xanthifolia	+				
Ambrosia psilostachya		+		+	
Heliopsis scabra	+	+		+	+
Rudbeckia hirta	+	+		+	+
Brauneria angustifolia	+				+
Lepachys columnaris				+	
Helianthus scaberrimus	+	+	+	+	+
Helianthus grosseserratus				+	
Helianthus giganteus	+	+			
Helianthus Maximiliani	+			+	
*Gaillardia aristata	+	+	+		+
Achillea millefolium	+	+	+	+	+
Artemisia caudata	+	+	+	+	
Artemisia dracunculoides	+	+			
Artemisia glauca	+	+			
Artemisia ludoviciana	+	+	+	+	+
Artemisia frigida	+	+	+	+	+
Cirsium undulatum	+	+	+	+	+
Lactuca canadensis	+		+		+

	I	II	III	IV	V
<i>Lactuca pulchella</i>	+	+	+	+	+
<i>Lygodesmia juncea</i>	+	+	+		+
<i>Agoseris cuspidata</i>	+		+		
* <i>Agoseris glauca</i>	+		+	+	
<i>Crepis runcinata</i>			+	+	
<i>Prenanthes racemosa</i>				+	+
<i>Hieracium canadense</i>	+	+	+	+	+



Map of the vicinity of Carberry.

PLATE VI



Fig. 1. A bit of native prairie on the west side of Carberry.

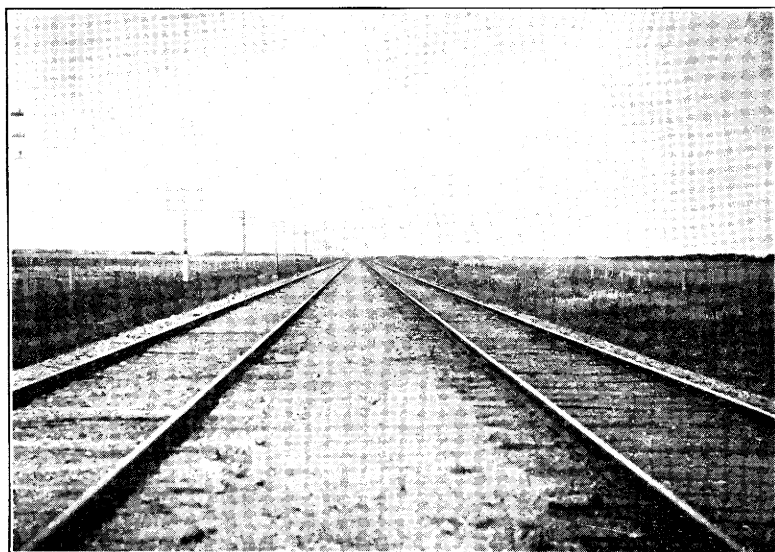


Fig. 2. Prairie along the Canadian Pacific Railway west of Carberry, looking west.

PLATE VII

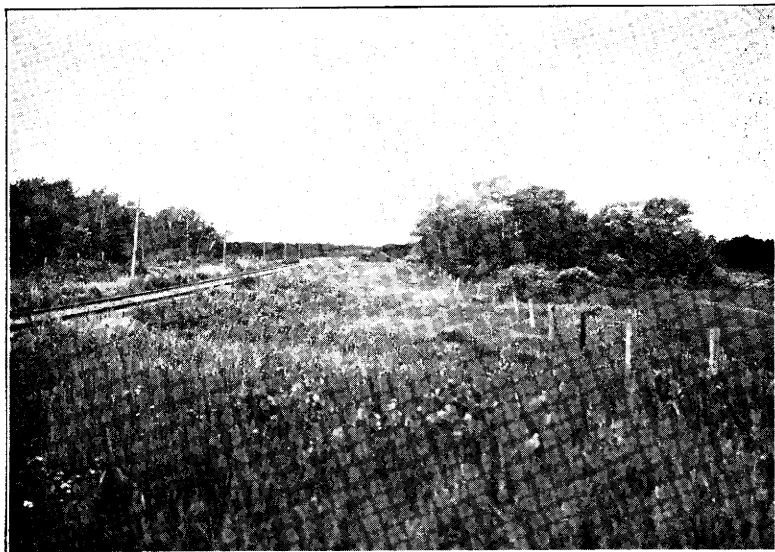


Fig. 1. Sandy prairie at Brandon Junction.

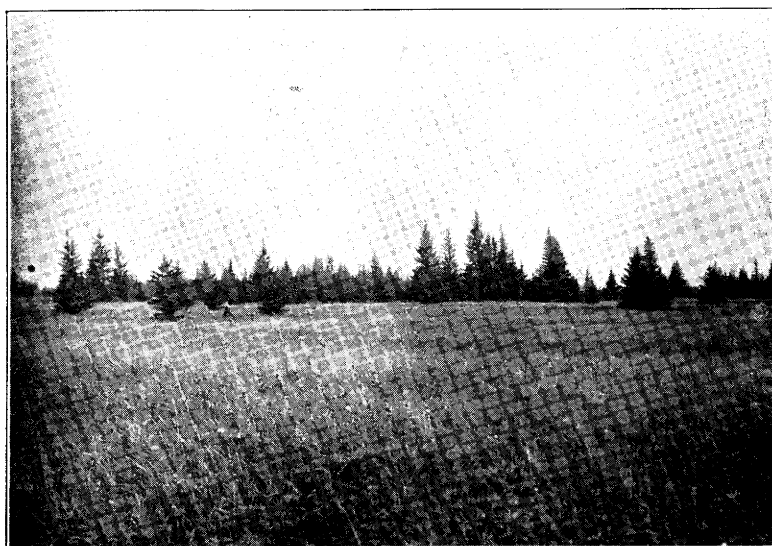


Fig. 2. Spruce Plain, with sandy plain and white spruce.

PLATE VIII



Fig. 1. Dunes east of Carberry. The two shadow-like areas are plants of *Juniperus horizontalis*. Bur-oak at left in foreground.

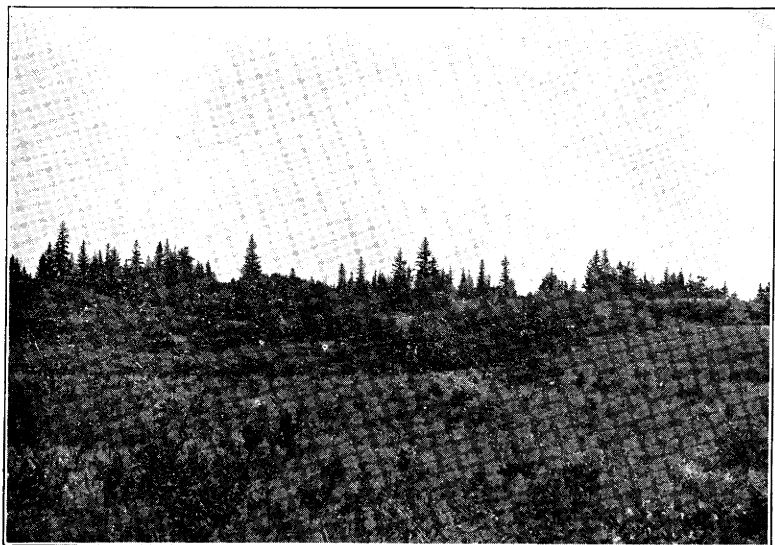


Fig. 2. Dunes east of Carberry, showing sandy prairie and white spruce.



UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

VOLUME XI

NUMBER 6

THE MYOLOGY OF SPHENODON PUNCTATUM

by

THEODORE C. BYERLY

PUBLISHED BY THE UNIVERSITY, IOWA CITY

Donna Miss. Lib.
ex
2-23-1926

THE MYOLOGY OF SPHENODON PUNCTATUM

INTRODUCTION

Due to the generosity of Prof. C. C. Nutting, the writer was allowed to dissect the muscles of two specimens of *Sphenodon punctatum* which were brought back by the Fiji-New Zealand Expedition of the summer of 1922. These specimens are of special interest since they belong to the only living species of Rhynchocephalia, the lowest of all the existing orders of the class Reptilia. The species is rapidly becoming extinct and careful myological studies should be made while it is still existant. Further emphasis is placed on such studies since, according to Cope's law of the unspecialized: "The perfection produced by each successive age has not been the source or parent of future perfection. The types which have displayed the most specialized mechanism have either passed away, or, undergoing no change, have witnessed the progress and ultimate supremacy of those which were once their inferiors."¹

Sphenodon is, of all living reptiles, probably the most closely allied to the amphibians on the one hand and the higher vertebrates on the other. Since this is true, one should expect *Sphenodon* to show more or less transitional stages between the unspecialized urodele condition found in the salamanders and the specialized form of creatures higher in rank than itself. Cope's law of the unspecialized seems pretty well substantiated by paleontological evidence, and it is generally accepted, so *Sphenodon* should possess characters very like those possessed by the progenitors of birds and mammals. According with this hypothesis, *Sphenodon* is very primitive in all its characters and no less so in its musculature.

Among the most interesting fields in myology is that of serial and special homology. *Necturus* has been used as the base form, by many workers, for determining serial and special homologies in limbed vertebrates and it is *Necturus* which has been used as a basis for such conclusions drawn in this paper. As a matter of fact, there is

¹ Cope, E.D., Origin of the Fittest, p. 234.

no one absolute basis for determining either serial or special homologies, unless it would be through a series of models prepared from serial sections of successive embryonic stages. Even these, were they available, would present very grave difficulties. However, since nerve supply for each muscle comes from the somite from which that muscle was derived, the nerve supply probably furnishes the most reliable criterion for the determination of homology. When the nerve supply is obscured by complex branching and anastomosis, as in the brachial plexus, muscle insertion must aid in the determination of homology. Arterial blood supply, origin and position must sometimes be considered but can by no means be regarded as reliable bases for judgment.

Homology of the muscles of the proximal portions of the limbs has long been a controversial subject among students of myology. It is hoped that a critical examination of the muscles of *Sphenodon* may contribute something to the solution of this difficult problem. Some investigators have homologized the great extensors of brachium and thigh (Quain); while others (Owen) homologize the extensors of the brachium with flexors of the thigh and vice versa. The difference of opinion is due to the opposite direction of flexion of the two limbs. The condition in *Sphenodon* is somewhat transitional between the unspecialized condition in the limbs of *Necturus* and the stereotyped stele-zeugopodial articulation in the higher reptiles and the mammals.

While the present attempt to homologize the muscles of *Sphenodon* serially in the limbs and especially with the muscles of *Necturus* will doubtless leave much to be desired, it is hoped that the dissections have been so carefully described and illustrated by diagrams that they will furnish a reliable basis for further work. This is especially true because, apparently, very few men have availed themselves of the opportunity actually to dissect a well-preserved specimen, and undoubtedly the opportunity will become rarer as the material becomes more difficult to obtain.

The most complete description of the muscles of *Sphenodon* is that of Osawa. This paper was published in 1899 and may be found in the "Archiv für Mikroskopische Anatomie," Bd. 51. It contains a complete description of the muscles and their nerve supply together with a partial list of serial and special homologies. His illustrations leave much to be desired and a few of his descriptions are incorrect.

The earliest account in the available literature is that of Gunther,

published in 1867. His account is accurate but covers only a few of the limb muscles and a partial dissection of the intercostal musculature. He took his nomenclature from anthropotomy and some of his special homologies will hardly stand. Gadow, 1887 and 1890, published very thorough accounts of the caudal musculature, including both drawings and discussion. Furbringer's paper, 1892, has been available through extracts made from it by Gregory and Camp in a paper published in the "Bulletin of the American Museum of Natural History," vol. 38. Gegenbaur (Leipzig, 1896) gives an account of the integumental musculature of the head and neck (after Ruge). For *Necturus*, Wilder's excellent account has been the chief reference.

Both specimens dissected for this account died of a bone and muscle necrosis diagnosed, with some doubt, as osteo-myelitis. The first specimen had a large necrotic mass on the dorsum of the left manus and the carpals of that member were nearly destroyed; the symphysis menti was also destroyed. After death it was skinned and preserved in five percent formalin. Dissection brought to light other necrotic masses in the m. pectoralis, in the liver and at the juncture of a regenerated caudal portion with the original body segments. The caudal region of both specimens was regenerated for the last fourteen or fifteen segments.

The second specimen became very ill in May 1923, was killed and the entire body was fixed in chrom-aceto-formaldehyde in order to preserve the tissues for histological work. The symphysis menti was destroyed by necrosis in this specimen.

The dissection of these members of an ancient race, occupying so important a position in any schema of the sequence of forms in the course of organic evolution, and so nearly extinct, has been of great interest. Perplexing differences between the specimens dissected and the work of other men, and some few differences between other workers, have come up from time to time and the suggestions of Dr. F. A. Stromsten, under whom this work was undertaken, have been very helpful in arriving at conclusions.

THE VISCERAL MUSCLES

The visceral muscles are located in the head and neck. They arise, embryologically, from the hypomeres rather than the epimeres. Phylogenetically, they are the survivals of the musculature of the gill arches of lower forms. In *Sphenodon*, they include the integu-

mental and facial musculature, the intrinsic muscles of the hyoid and larynx, and the muscles of mastication.

"Following² the lines laid down by Gegenbaur in his 'Lehrbuch der Anatomie der Menschen', on the origin of the facial muscles, G. Ruge has made detailed researches on the facial musculature of lemurs, from which he arrives at the following results:

The fact that all the muscles supplied by the facial nerve belong to the same series indicates that those related to the visceral skeleton, and having originally nothing to do with the face, which are supplied by the same nerve, must have shifted upwards from the region of the lower jaw and neck, so as to come into close relation with the soft parts surrounding the apertures of the ear and mouth, that is, to the secondarily formed lips and to the external ear. From these points, they extended further, taking on new relations to the eye, nasal aperture and to the frontal and temporal regions, those behind it from the occipital region. The upward change of the position of the musculature thus took place along two lines,—in front of, and behind the ear, as is proved by its innervation, ...

. . . . The platysma myoides thus forms the matrix for the facial muscles, and it represents the remnants of a musculature continued forward to the head, which has retained (e.g. in man) an undifferentiated form in the neck (Gegenbaur).

Besides the platysma myoides there is a second deeper dermal system of muscles in the neck, the sphincter colli. This, like the platysma, also takes on secondary relations to the head, and gives origin to the levator labii-superioris proprius, levator anguli oris, sphincter oris, buccinatorius and the proper muscles of the nose. The facial muscles not named here arise from the platysma."

Gegenbaur³ mentions the facial musculature in *Sphenodon* in connection with Ruge's work and gives one text figure.

"Einen sehr primitiven Zustand bietet der Facialismuskulatur bei *Sphenodon*, wo alle Theile noch im Zusammenhang stehen. An den noch weit oben entspringenden Abductor mandibulæ schlieben sich Zuga (Sphincter dorsalis) die ventral in den Intermandibularis sich fortsetzen, und daran reihen sich weiter abwärts entspringende Bündel, welche in den schwachen Sphincter colli fortgesetzt sind."

Sphenodon presents, in the adult, a very primitive condition of the facial musculature. Except for a few fibers in the eyelids, constituting an orbicularis oculi, there is little differentiation of the primitive muscle sheet. This sheet is continuous ventrally from the shoulder region to the symphysis menti. The posterior portion may be termed the sphincter colli and that between the rami of the mandible, the intermandibularis. The antero-dorsal portion is contigu-

² Wiedersheim, R., Comparative Anatomy of Vertebrates, p. 121.

³ Gegenbaur, C., Vergleichende Anatomie der Wirbelthiere, p. 631.

ous with the depressor mandibulæ (abductor mandibulæ of Gegenbaur) and passes anterior to the membrana tympani; Gegenbaur terms this the sphincter dorsalis.

VISCERAL MUSCLES OF THE HYOID REGION

This group includes: m.mylohyoideus, m.stylohyoideus, m.cerato-hyoideus and the proper muscles of the larynx.

MYLOHYOIDEUS

This muscle lies dorsal to the anterior portion of the intermandibularis and is pretty well differentiated from it. It forms a thin but strong sheet of muscle fibers which stretches between the anterior third of the rami of the mandibles. With the intermandibularis, it serves to raise the floor of the mouth.

Innervation: N. trigeminus.

STYLOHYOIDEUS

This is a very small muscle that stretches from the styloid process to the lateral border of the posterior portion of the cerato-hyal; levator of the hyoid.

Innervation: N. facialis.

CERATOHYOIDEUS

This muscle lies between the lateral border of the geniohyoideus and the mesial surface of the pterygoideus internus. It extends from the anterior border of the postero-lateral portion of the hyohyoid to the mesial part of the antero-lateral portion of the cerato-hyoid.

Innervation: N. facialis.

MUSCLES OF THE LARYNX

These muscles present no specialization in *Sphenodon*; they consist of a single constrictor and a pair of dilators.

DILATORES LARYNGEI

These consist of a pair of muscles, one on either side of the larynx. Each extends from its origin on the cricoid to its insertion on the antero-lateral surface of the arytenoid. By abduction of the arytenoids, they serve as dilators of the larynx in inspiration.

CONSTRUCTOR LARYNGEUS

Except for a very short distance on the mid-dorsal surface, this muscle completely surrounds the larynx. It covers almost the entire

surface of the arytenoid cartilages from which its fibers are exerted and into which they are inserted.

Innervation: N. vagus.

MUSCLES OF MASTICATION

Sphenodon is largely predaceous in its food habits. It eats lizards, bones and all, so one might expect to find rather heavy muscles of mastication. The jaws are very strongly muscled, the pterygoideus internus being exceptionally heavy. The group consists of three adductors, m. temporo-massetericus, m. pterygoideus externus, m. pterygoideus internus and a single abductor, m. depressor mandibulæ.

TEMPORO-MASSETERICUS

This muscle is homologous with both the temporalis and the massetericus of more specialized animals. It forms a heavy muscle mass which lies beneath the superficial fascia and the temporal arcade on the postero-lateral surface of the head.

Origin: From the fascia which covers the lateral temporal fossa and from the inner surfaces of the squamosal, jugal and postorbital bones, its fibers extend ventrally to their

Insertion: As muscle fibers, on the coronoid process and the subjacent dorso-lateral surfaces of the dentary and supra-angular bones. There is some indication of division into external and internal masses at the point of insertion.

Action: Closes the mouth; it is most efficient when the mouth is almost closed.

Innervation: N. trigeminus.

PTERYGOIDEUS EXTERNUS

This muscle is not sharply defined from the preceding but its fibers run at a somewhat different angle. It lies just beneath the temporo-massetericus.

Origin: From the inner surface of the postorbital, the lateral surface of the epipterygoid, and from the fascia which covers the supratemporal fossa, its fibers extend postero-laterally to their

Insertion: On the dorso-mesial surface of the supra-angular.

Action: Aids in closing the mouth and in the grinding action when the mouth is almost closed.

Innervation: N. trigeminus.

PTERYGOIDEUS INTERNUS

This is the heaviest and most powerful of the muscles of mastication.

tion. It is the innermost of the group and forms a large rounded protuberance into the mouth cavity.

Origin: From the basi-sphenoid, the parietal, the pterygoid and from the fascia covering the supra-temporal fossa.

Insertion: On the ventral and lateral surfaces of the dentary.

Action: Abductor of the mandible, most efficient when the mouth is widely gaping.

Innervation: N. trigeminus.

DEPRESSOR MANDIBULÆ

This muscle follows the posterior contour of the squamosal and lies just beneath the sphincter colli, except in the region near the dorsal mid-line where it is covered by the aponeurosis of the cranial portion of the trapezius.

Origin: From the dorsal portion of the posterior surface of the squamosal and the lateral portion of the posterior surface of the parietal.

Insertion: On the posterior and ventral surfaces of the articulare.

Action: Abductor of the mandible.

Innervation: N. facialis.

THE AXIAL MUSCULATURE

The axial musculature of *Sphenodon* is perhaps more significant than the appendicular. The intercostal system is almost as complex as that of the Ophidia, due to the presence of movable and perhaps functional ribs or gastralea on the abdominal surface. The muscles that function in respiration show many characters transitional between the simple Urodele type and the condition found in the more specialized reptiles. A m. triangularis sterni is differentiated from the⁴ transversalis sheet; this fact is one of many which may serve to indicate that *Sphenodon* is very close to both bird and mammal forms in its myology.

The usual differentiation into dorsal and ventral groups is quite marked. The following muscles have been considered as belonging to the ventral axial group but there are a few others, discussed under the trunco-zonal muscles of the appendicular group, which might be considered here: m. geniohyoideus, m. genioglossus, m. hyoglossus, m. cleido-episterno-hyoideus, m. omohyoideus, m. sterno-coracoideus

⁴ In discussing the myology of birds, Wiedersheim says; "External and internal intercostals are well developed, and a triangularis sterni appears for the first time on the inner surface of the sternal ends of the ribs." Wiedersheim, R., Comparative Anatomy of Vertebrates, p. 140.

superficialis, m. sterno-coracoideus profundus, m. costo-sterno-scapularis, m. costo-coracoideus, m. serratus posterior, m. serratus anterior, m. rectus abdominis externus, m. rectus abdominis internus, m. obliquus externus, m. obliquus internus, m. transversalis abdominis, m. triangularis sterni, mm. intercostales externi longi, mm. uncini-costales longi, mm. uncini-costales breves, mm. intercostales externi breves, mm. intercostales interni breves, mm. intercostales interni longi, mm. intercostales ventrales, mm. abdomino-costales, m. longus colli, m. ilio-sacro-costo-costalis, m. ilio-ischio-caudalis.

GENIOHYOIDEUS

Origin: From the inner surface of the mandible, from a space a quarter inch in width just laterad of the symphysis. Its fibers extend caudad beneath the intermandibularis to their

Insertion: On the anterior border of the medial half of the hyoid.

Action: Draws the hyoid forward; perhaps aids in protrusion of the tongue.

GENIOGLOSSUS

Origin: From the inner surface of the mandible, just dorsal to the origin of the geniohyoideus.

Insertion: On the ventral surface of the tongue; its fibers mingle with those of the lingualis.

Action: Aids in manipulation and protrusion of the tongue.

HYOGLOSSUS

Origin: From the anterior border of the hyoid, beneath the middle portion of the geniohyoid. Its fibers extend anteriorly to their

Insertion: On the ventral surface of the tongue, about an inch from the tip.

Action: It serves as a retractor of the tongue, opposing the action of the geniohyoideus.

These three muscles have been discussed with the ventral axial muscles in spite of the fact that they are frequently considered with the visceral muscles. Wilder⁵ makes the following statement: "The musculature of the tongue, especially its extrinsic muscles, such as hyoglossus, genioglossus, styloglossus, etc., is probably derived from the visceral muscles, . . ." On the other hand, Ecker,⁶ in describing the course of the hypoglossal nerve in the frog, states: "N. hypoglossus or n. spinalis I. (A)—(B)—(C) When near the glosso-

⁵ Wilder, H.H., History of the Human Body, p. 216.

⁶ Ecker, A., Anatomy of the Frog, p. 182.

pharyngeal it supplies twigs to the geniohyoideus, sternohyoideus and omohyoideus. (D) One of the branches passes inward to supply the hyoglossus." Sobotta,⁷ in his work on human anatomy, says: "The geniohyoid is supplied by fibers from the first and second spinal nerves which accompany the hypoglossal nerve." In *Sphenodon*, the hypoglossal furnishes the nerve supply for the geniohyoideus, genioglossus and hyoglossus. Since the n. hypoglossus is not yet established as one of the cranial nerves in the Anura, and since it does not supply a branchial arch at any time, it seems logical to assume that in *Sphenodon* those muscles which it supplies should be considered with the ventral axial muscles.

If this postulate be accepted, there is in *Sphenodon*, as one might expect in a primitive form so close to the Urodeles, an almost unbroken, ventral, longitudinal muscle sheet extending from the posterior border of the ischiadic plate to the symphysis menti. It includes the following muscles which are probably serially homologous: m. geniohyoideus, m. hyoglossus, m. genioglossus, m. cleido-episternohyoideus, m. sterno-coracoideus superficialis, m. sterno-coracoideus profundus, m. rectus abdominis externus, m. rectus abdominis internus.

CLEIDO-EPISTERNO-HYOIDEUS

This is a thin muscle which covers most of the ventral surface of the œsophagus and trachea. Its fibers run postero-anteriorly just beneath omohyoideus and the sphincter colli.

Origin: From the anterior border of the mesial half of the clavicle and from the whole anterior border of the episternum.

Insertion: On the posterior border of the lateral half of the hyoid cartilage, beneath and lateral to the insertion of the omohyoideus.

Action: Retractor of the hyoid.

OMOHYOIDEUS

This muscle and the preceding one act as depressors and retractors of the hyoid, thus serving to oppose the action of the geniohyoideus and ceratohyoideus and to maintain a stable point of origin for the hyoglossus.

Origin: It takes origin from the antero-medial portion of the mesial surface of the scapula, just dorsal to the articulation of that bone with the clavicle, and from the scapulo-coracoid ligament. It

⁷ Sobotta, J., Atlas and Textbook of Anatomy, p. 212.

curves ventro-anteriorly passing dermad of the cleido-episterno-hyoideus to its

Insertion: On the medial surface of the hyoid.

STERNO-CORACOIDEUS SUPERFICIALIS

The various elements of the pectoral girdle are not fused to form a solid, inflexible unit in *Sphenodon* as they are in the Anura and the more highly specialized reptiles. The sternum and coracoid are quite free from each other as far as bony or cartilaginous connections are concerned. The T-shaped episternum (interclavicularis) anchors the clavicles, coracoids and sternum rather loosely in place but permits a considerable amount of interplay. This interaction is controlled in part by the sterno-coracoideus superficialis.

Origin: It takes origin from the medial half of the extreme posterior portion of the inner surface of the sternum. Its fibers extend in a thin sheet about a half inch in width, antero-laterally to their

Insertion: On the coracoid, along the medial border of the epicoraco-humeralis.

STERNO-CORACOIDEUS PROFUNDUS

This muscle lies just ventral to the sterno-coracoideus superficialis but is somewhat wider, extending laterally to fuse with the costo-coracoideus. Together with the muscle just described, it aids in retraction of the coracoid and unification of the pectoral girdle.

Origin: From the anterior border of the sternum, beneath the sterno-coracoideus superficialis. Its fibers extend cephalad to their

Insertion: Ventral and mesial to those of the sterno-coracoideus superficialis, along the medial border of the epicoraco-humeralis.

COSTO-STERNO-SCAPULARIS

This muscle is probably serially homologous with the intercostales ventrales.

Origin: From the anterior border of the first complete rib, just ventral to the ventro-mesial curvature of that rib; it extends cephalad to its

Insertion: On the dorsal third of the sterno-scapular ligament and thence on the mesial surface of the ventral portion of the scapula.

Action: Retractor of the scapula, compressor of the ribs.

COSTO-CORACOIDEUS

This muscle lies mesial to the costo-sterno-scapularis beneath the

sterno-coracoideus superficialis, and lateral to the sterno-coracoideus profundus.

Origin: It takes origin from the anterior border of the first complete rib, just mesial to the origin of the costo-sterno-scapularis. It extends cephalad to its

Insertion: On the mesial face of the coracoid, between the junction of the subscapular and the coracoid heads of the subscapulo-coraco-humeralis.

Action: Retractor of the scapula, compressor of the ribs.

RECTUS ABDOMINIS EXTERNUS

This muscle is divided into segments by the abdominal ribs and is further indistinctly divided into a superficial and a deeper layer. The external layer has many fibers which insert into the integument.

Origin: This muscle takes origin from the whole posterior border of the ischium. It is a little difficult to say certainly which end of this muscle is its origin and which its insertion but since the pelvic girdle is more or less firmly fixed and the pectoral girdle is flexible, the origin as stated is the more probable. It extends anteriorly over the origin of the pubo-ischio-tibialis and continues to its

Insertion: On the entire posterior border of the sternum.

RECTUS ABDOMINIS INTERNUS

Origin: It takes origin from the lateral tuberosity of the pubis and from an accessory ligament which extends between the rectus abdominis externus and the pubo-ischio-tibialis to the pubic symphysis. It extends antero-mesially to its

Insertion: On the internal midline of the abdominal ribs and on the inner surface of the rectus abdominis externus.

OBLIQUUS EXTERNUS

The obliquus externus forms a continuous sheet from the pelvic girdle anterior to the first or second rib, where it becomes modified to form a part of the serratus group. It is indistinctly divided into a superficial and a deep layer, the fibers of both running in the same direction and having almost the same origin and insertion.

Origin: By digitations from each of the complete ribs, after the second, and from the lumbar fascia; the fibers of both sheets pass ventro-laterally to their

Insertion: By muscle fibers on each of the abdominal ribs and by a strong ligament on the lateral tuberosity of the pubis laterad to the rectus internus.

OBLIQUUS INTERNUS

The obliquus internus shows very clearly that it has only recently, phylogenetically speaking, been broken into transversalis and obliquus. It does not form a complete sheet over the entire inner abdominal wall, but covers only the dorso-mesial portion of it. It lies just retro-peritoneal and the peritoneum adheres very closely to it.

Origin: By tendinous digitations from the centra of each of the vertebræ from the tenth to the twenty-fifth. It extends antero-laterally to its

Insertion: By muscle fibers on each of the complete ribs, for a space about a quarter inch in length on the posterior border, about an inch laterad from the centrum and two intercostal spaces anterior to the vertebra of origin.

TRANSVERSALIS ABDOMINIS

The transversalis abdominis sheet lies lateral to the obliquus internus and just beneath the peritoneum, except at the anterior end where it passes behind the triangularis sterni. The peritoneum adheres to it very tightly.

Origin: From each of the complete ribs by digitations which take origin just lateral to the insertions of the obliquus internus and from the lumbar fascia in the lateral line region. The fibers extend ventrally to their

Insertion: On the peritoneum along a very even line just at the ventro-internal terminations of the costæ and on the sternum, just laterad to the insertion of the triangularis sterni.

TRIANGULARIS STERNI

This muscle forms a sheet about a half inch in width just mesiad from the transversalis sheet. Its presence has not been recorded by others who have worked on *Sphenodon* but it forms a very distinct muscle whose fibers cross those of the transversalis abdominis in a markedly distinct direction.

Origin: It takes origin from the last incomplete rib, that of the eighth vertebra, and from the first complete rib, from the postero-medial border between the insertion of the obliquus internus and the origin of the transversalis abdominis.

Insertion: On the inner surface of the sternum, along the lateral border of the sterno-coracoideus profundus.

MUSCLES OF THE RIBS AND SCUTES

There is some difference of opinion among men who have worked on *Sphenodon* as to the use or non-use of the ventral scutes in locomotion. From observation of the movements of the creatures it would seem that they may use these scutes as auxiliary means of movement. This observation is much strengthened by dissection of the musculature. The abdomino-costales tilt the scutes so that they form an efficient friction surface. Contraction of the external oblique series of muscles would slowly project the body forward, using the scutes as fixed points by their contact with the ground. Since *Sphenodons* inhabit burrows, this action would be of considerable service to them in progress through narrow places where use of the limbs would be impeded.

INTERCOSTALES EXTERNI LONGI

Just beneath the obliquus externus lie two sets of semisegmental muscles whose fibers run in the same direction as those of the obliquus externus. The more ventral series, which consists of the intercostales longi, is rather irregular in occurrence but fairly regular in form.

Origin: It is formed by a number of slips, each of which rises from the posterior border of the lower medial portion of a rib, extends backward and downward over the rib next posterior to its origin to its

Insertion: On the anterior border of the second rib posterior from the origin, just dorsal to the antero-ventral curvature of that rib. Such slips do not rise regularly from every rib but do so fairly regularly from the more anterior ribs, after the first, and less regularly from the more posterior.

UNCINO-COSTALES LONGI

This muscle sheet forms the dorsal series of the second layer of the oblique musculature.

Origin: Each slip rises from the posterior border of the proximal half of an uncinate process and a small area of the rib adjacent. Each slip extends postero-ventrally over the rib next posterior, to its

Insertion: On the rib second posterior to the origin, just dorsal to the insertion of the intercostales externi longi.

UNCINO-COSTALES BREVES

This series is rather more regular in form and occurrence than the two preceding but, belonging to the same muscle layer, forms a

third series of semisegmental muscles, each slip of which extends from its

Origin: On the ventral border of an uncinat process to its

Insertion: On the lateral border of the rib next posterior to its origin, on a space about a fourth inch in length just ventral to the uncinat process.

INTERCOSTALES EXTERNI BREVES

These muscles form the usual thin sheet with fibers running diagonally dorso-ventral from the posterior border of one rib to the anterior border of the one next posterior.

ABDOMINO-COSTALES

Slips from the inner surface of the rectus abdominis and from the gastralea attach to the posterior border of the external surface of the ventral portion of each rib.

INTERCOSTALES VENTRALES

The ventral portions of the intercostal spaces are without fibers of the intercostales externi breves. Ventral to the sharp antero-ventral curvature of the ribs, many loosely bound fascicles of muscle fibers extend from one rib to the next. These fascicles run from a higher posterior origin to a slightly lower anterior insertion on the next rib. Some of these fibers traverse the outer surface of the rib of their insertion to insert on its anterior border.

INTERCOSTALES INTERNI BREVES

This muscle sheet might be construed to include the intercostales ventrales. Its fibers traverse the intercostal spaces in the same direction but dorsal to the preceding. They lie just internal to the intercostales externi breves.

INTERCOSTALES INTERNI LONGI

This series consists of a slip for each rib after the second. A stout tendinous sheet from the ilium serves as origin for the slips to the last two ribs.

Origin: The muscle slips comprising this muscle take origin from the anterior border of each rib for a space about a half inch long just below the point of origin of the ilio-sacro-costo-costalis slip and the insertion of the obliquus internus slip and then run antero-ventrally to their

Insertion: On the posterior border of the rib second anterior from the rib of origin, just dorsal to the antero-ventral curvature of that rib.

RESPIRATION IN SPHENODON

The change from aquatic to terrestrial habits required, of course, considerable readjustment of the trunk musculature to make lung breathing possible. The Urodeles, living a sluggish semi-aquatic life, are never more than partially dependent on their lungs for oxygen supply, and as a consequence need very little specialization for lung breathing. Even in the more active Anura, which characteristically spend a major portion of their adult existence on land, most of the oxygen supply is obtained through the skin and œsophago-pharyngeal surfaces. Not until the dry skinned, terrestrial dwelling reptiles are reached in the phylogenetic scale, do the lungs assume a rôle of major importance in respiration.

Sphenodon is the most primitive of the existing Reptilia; so one might postulate that in *Sphenodon* might be found a situation almost exactly transitional between the Amphibia and the higher terrestrial vertebrates. This is exactly the condition they present in dissection. Instead of a simple segmented muscle sheet forming the body wall, there appears quite an intricate, but not wholly regular group of series of muscle slips which act as levators and depressors of the ribs.

The following muscles act as levators of the ribs: m. obliquus externus, mm. uncini-costales breves, mm. uncini-costales longi, mm. intercostales externi longi, mm. intercostales externi breves.

They are opposed by the following depressors and compressors of the ribs: depressors; mm. intercostales interni breves, mm. intercostales interni longi, m. obliquus internus, mm. intercostales ventrales; compressors; m. triangularis sterni, m. transversalis abdominis. The rectus abdominis internus may aid in respiration as a compressor of the body cavity.

Since both specimens had already been used in the preparation of a paper on the digestive system, a careful study of the diaphragm was impossible. As far as could be ascertained, it was incomplete and not muscular.

LONGUS COLLI

Origin: From the ventral surfaces of vertebræ two to twelve inclusive and from their transverse processes, a slip from the rib of

the seventh vertebra; it extends cephalad, just lateral to the median line, to its

Insertion: On the ventral surfaces of the axis and the occipital condyle.

Action: Aids in lateral movements of the head and in holding it erect.

ILIO-SACRO-COSTO-COSTALIS

Origin: From the ilium, the sacrum, the ribs, and by fibers from the longus colli.

Insertion: On the transverse processes and centra of all the vertebræ anterior to the sacrum.

Action: Flexor and tensor of the trunk.

Remarks: This muscle seems to be unique in its continuation anteriorly beneath the ribs. Its posterior portion is probably homologous with the quadratus lumborum of higher forms.

ILIO-ISCHIO-CAUDALIS

Origin: From the ilium, the ischium and from the ventral surfaces of the transverse processes of the caudal vertebræ.

Insertion: On the transverse and hæmal processes of the caudal vertebræ.

Action: Abductor-adductor of the tail.

DORSAL AXIAL MUSCLES

This group includes all the axial muscles dorsal to the lateral line and above the ribs. These muscles are not in all cases clearly separated from one another and their description is somewhat problematical, their designation more or less arbitrary. The group is customarily divided into a median and a lateral portion; this plan has been followed as far as practicable. The medial group includes the m. semispinalis capitis, m. transverso-spino-spinalis, mm. interspinales. The lateral group includes the m. cervico-capitis, m. sacro-transverso-transversalis, m. caudæ dorsalis, m. obliquus capitis, m. rectus capitis posticus.

Medial

SEMISPINALIS CAPITIS

Origin: From the antero-lateral surfaces of the spinous processes of the fourth to eighth cervical vertebræ inclusive, it runs cephalad to its

Insertion: On the dorsal portion of the posterior surface of the parietal.

Action: Aids in lateral and dorsal movements of the head.

TRANSVERSO-SPINO-SPINALIS

Origin: This muscle receives many fibers from the sacro-transverso-transversalis from which it is not sharply defined. Most of its fibers take origin from the spinous processes of vertebræ three to twenty-six and from the proximal portions of their transverse processes.

Insertion: The deepest layer of fibers inserts on the spinous process of the vertebra second anterior to their origin; the fibers of the middle layer skip two vertebræ to insert on the spinous process of the vertebra third anterior from their point of origin; the fibers of the superficial layer unite with fibers of the sacro-transverso-transversalis and insert on the vertebra sixth anterior to their origin.

Action: Serves as a flexor of the body.

INTERSPINALES

Origin: From the anterior surfaces of the spinous processes of all the vertebræ.

Insertion: On the posterior border of the spinous process of the vertebra next anterior to the point of origin.

CAUDÆ DORSALIS

Origin: There is no break between this muscle and the sacro-transverso-transversalis but its position makes separate consideration necessary. It takes origin from the sacrum, the ilium, and the spinous and transverse processes of the caudal vertebræ and extends caudad to its

Insertion: On the spinous and transverse processes of the caudal vertebræ.

Action: Flexor of the tail.

Lateral

CERVICO-CAPITIS

Origin: From the lateral surface of the neck at the level of the sixth vertebra and from the transverse process of that vertebra; by fibers from the sacro-transverso-transversalis. It extends superficially to its

Insertion: On the posterior border of the squamosal.

Action: Aids in lateral and dorsal movement of the head.

SACRO-TRANSVERSO-TRANSVERSALIS

Origin: From the sacrum, from the anterior border of the ilium, from the transverse processes of vertebræ three to twenty-six, from the anterior surfaces of the dorsal portions of all the ribs and from the dorsal surfaces of the uncini.

Insertion: For the most part, on the transverse processes and ribs from the axis to the sacrum. From the level of the fourth, fifth, sixth and seventh vertebræ, four more or less distinct slips arise which insert on the occipital condyle, the axis, the atlas and the tip of the transverse process of the third cervical vertebra.

Action: Flexor of the body.

OBLIQUUS CAPITIS

Origin: This muscle is differentiated from the sacro-transverso-transversalis at about the level of the fourth vertebra. It takes origin from the transverse processes of vertebræ three, four and five.

Insertion: On the ventral portion of the posterior border of the squamosal and on the posterior border of the exoccipital.

Action: Aids in lateral movements of the head.

RECTUS CAPITIS POSTICUS

Origin: From the spinous processes and dorsal surfaces of the axis and atlas.

Insertion: On the posterior surfaces of the squamosal and occipital.

Action: Aids in lateral movement of the head.

Innervation: All the dorsal axial muscles are supplied by the rami dorsales of the spinal nerves.

THE APPENDICULAR MUSCLES

Sphenodon is a very sluggish creature and since it is phylogenetically so close to the Amphibia, its limb muscles present few specializations. In the forelimb, the olecranon process is present making the direction of flexion fixed; in the posterior limb, however, there is no osseous differentiation to fix the direction of flexion of the crus on the shank. The direction of flexion in the hind limb is fixed only by the position of muscle insertions, as is the case in the Urodeles. *Sphenodon* thus presents a perfect transitional stage between the Urodeles and the more highly specialized reptiles, birds and mammals which have the direction of flexion between the first and second segments of both limbs fixed by osseous differentiations.

This is a very important fact from the viewpoint of serial homology for, since the forelimb has attained the form characteristically presented in the higher, limbed vertebrates, and the hind limb still remains in a rather generalized condition, it should be possible to determine certainly whether the extensor groups of the two limbs are or are not serially homologous. This probability is further strengthened by the fact the hind limb is just sufficiently fixed in its action to make possible an irrefutable numbering of the digits.

The sluggish habits of the creatures have not made the development of a powerful extensor of the digits necessary. As a result, the muscle of the antibrachium homologous to the dorsalis antibrachialis of *Necturus*, m. extensor communis digitorum, is in no way specialized. The extensor communis of the hind limb has progressed a little way and sends a tendon along the lateral surfaces of the third and fourth digits. The flexors of both limbs are well developed, as one might expect since *Sphenodon* is a burrowing animal. The rotators of the femur are very well developed to oppose the action of the powerful caudal muscles. Throughout the appendicular musculature of *Sphenodon*, there occur many accessory tendons, perhaps make-shift adaptations to a changing environment.

Both the specimens dissected had lost and regenerated the last twelve or fourteen caudal segments.⁸ This regenerated portion was very interesting because the regeneration was far from perfect. The regenerated portion showed no segmentation whatever. Instead of vertebræ, a hollow cartilaginous rod was formed into which the spinal cord did not penetrate. Between the last vertebra and the regenerated portion of the first specimen studied, there was a necrotic mass about the size of a pea. The muscle fibers in the regenerated portion were arranged in fasciculi which ran its entire length. The interstices were filled with firm fatty connective tissue.

CLASSIFICATION OF THE LIMB MUSCLES

In classifying the limb muscles, the method devised by Bolk will be used.

Anterior Limb

Truncozonal: dorsal; m. serratus anticus, m. levator scapulæ dorsalis superficialis, m. levator scapulæ ventralis superficialis, m. trapezius, m. cephalo-clavicularis; ventral; m. costo-coracoideus, m.

⁸ Byerly, T.C., Note on the Partial Regeneration of the Caudal Region of *Sphenodon punctatum*. Anat. Record, Jan. '25.

costo-sterno-coracoideus, m. serratus posterior, m. rectus abdominis externus, m. rectus abdominis internus.

Trunco-stelepodial: dorsal; m. latissimus dorsi; ventral; m. pectoralis.

Zono-stelepodial: dorsal; m. dorsalis scapulæ, m. epicoraco-humeralis, m. scapulo-humeralis anterior, m. scapulo-humeralis posterior, m. subscapulo-coraco-brachialis, m. cleido-humeralis; ventral; m. coraco-brachialis brevis, m. coraco-brachialis medius, m. coraco-brachialis longus, m. supracoraco-humeralis.

Zono-zeugopodial: dorsal; m. anconeus medialis; ventral; m. coraco-antibrachialis.

Stele-zeugopodial: dorsal; m. humero-radialis, m. anconeus lateralis, m. anconeus brevis, m. supinator longus, m. anconeus quartus; ventral; m. humero-antibrachialis, m. pronator teres.

Stele-actinopodial: dorsal; m. extensor carpi radialis, m. extensor carpi ulnaris; ventral; m. flexor carpi radialis, m. flexor carpi ulnaris.

Zeugo-phalangopodial: dorsal; m. supinator brevis; ventral; none.

Interzeugopodial: dorsal; none; ventral; m. pronator quadratus.

Stele-phalangopodial: dorsal; m. extensor communis digitorum; ventral; m. flexor communis digitorum.

Basi-phalangopodial: dorsal; mm. extensor communis digitorum breves, m. extensor pollicis brevis; ventral; mm. flexores communis digitorum breves, mm. lumbricales, mm. adductores communis, m. flexor pollicis, m. abductor pollicis, m. abductor digiti minimi, opponens digiti minimi.

Actino-phalangopodial: dorsal; mm. interossei dorsales; ventral; mm. interossei dorsales.

Posterior Limb

Trunco-zonal: dorsal; m. ilio-sacro-transverso-transversalis and m. caudæ dorsalis might be placed under this head but fall more properly under the head of dorsal axial musculature because they are innervated by the dorsal rami of the spinal nerves and the dorsal rami never supply limb muscles in higher forms; ventral; m. ilio-sacro-costo-costalis and m. ilio-ischio-caudalis have already been discussed under the ventral axial musculature, m. caudi-femoralis, m. caudi-ischio-tibialis, m. ischio-caudalis.

Zono-stelepodial: dorsal; m. ilio-femoralis, m. ischio-trochan-

tericus, m. pubo-ischio-femoralis internus; ventral; m. pubo-ischio-trochantericus, m. pubo-femoralis, m. ischio-femoralis.

Zono-zeugopodial: dorsal; m. extensor ilio-tibialis, m. ambiens, m. ilio-fibularis; ventral; m. pubo-ischio-tibialis, m. pubo-tibialis, m. ischio-tibialis posticus.

Stele-zeugopodial: dorsal; m. femoro-tibialis; ventral; m. gastrocnemius.

Stele-phalangopodial: dorsal; m. extensor communis digitorum; ventral; m. flexor communis longus digitorum.

Zeugo-basipodial: dorsal; m. tibialis anticus, m. peroneus, m. fibulo-tarsale 4; ventral; m. tibialis posticus.

Zeugo-phalangopodial: dorsal; m. abductor et extensor hallucis longus.

Interzeugopodial: m. pronator quadratus.

Basi-phalangopodial: dorsal; mm. extensores breves digitorum, m. abductor et extensor minimi digiti; ventral; mm. lumbricales, mm. adductores communis, mm. flexores breves digitorum, mm. abductores hallucis et secundi.

INNERVATION OF THE LIMB MUSCLES

Designation of the source of nerve supply for each muscle is made by indicating the number or numbers of the spinal nerves contributing. All the foregoing muscles designated as dorsal are supplied by dorsal branches of the ventral rami of the spinal nerves indicated while those designated as ventral are supplied by ventral branches of the ventral rami. The nerves are numbered consecutively from anterior to posterior in preference to the application of names taken from human anatomy.

Anterior Limb

Trunco-zonal—Dorsal

SERRATUS ANTICUS

This muscle consists of four slips from the level of vertebræ six, seven, eight, and nine. Its slips take their

Origin: From the fascia overlying the ilio-sacro-transverso-transversalis at the lateral line level. They extend dorsad, overlapping somewhat, to their

Insertion: On the dorsal border of the suprascapula.

Action: Adductor and levator of the scapula.

Innervation: Nn. spinales 6, 7, 8, and 9.

COLLI-SCAPULARIS

This muscle occupies a similar position in the fifth body segment. It is a levator of the scapula.

LEVATOR SCAPULÆ DORSALIS SUPERFICIALIS

Origin: From the anterior two-thirds of the lateral surface it runs cephalad beneath the trapezius to converge with the levator scapulæ ventralis superficialis and to its

Insertion: On the transverse process of the axis.

Action: Levator of the scapula; aids in lateral movement of head.

Innervation: Nn. spinales 2 and 3.

LEVATOR SCAPULÆ VENTRALIS SUPERFICIALIS

Origin: From the anterior portion of the mesial surface of the scapula above the origin of the trapezius, it runs cephalad to its

Insertion: By a slip to the transverse process of the axis and by a second slip on the transverse process of the third vertebra.

Action: Levator of the scapula and abductor-adductor of the head.

Innervation: Nn. spinales 2 and 3.

TRAPEZIUS

This muscle forms a broad, superficial sheet which covers the dorsal two-thirds of the side of the neck, extending caudad as far as the seventh vertebra.

Origin: From the temporal arch, dermad of the depressor mandibulæ, and from the fascia of the dorsal midline, its fibers converge to their

Insertion: On the dorsal third of the anterior border of the scapula.

Action: It is a protractor of the scapula and aids somewhat in holding it in place.

Innervation: Nn. spinales 2, 3, and 4.

CEPHALO-CLAVICULARIS

This muscle is analogous and probably homologous with the cleidomastoid of higher forms.

Origin: From the posterior border of the dorsal portion of the squamosal beneath the depressor mandibulæ. Its fibers extend ventro-caudally to their

Insertion: On the anterior border of the clavicle, ventral to the insertion of the trapezius.

Action: Levator of the scapula, abductor-adductor of the head.

Innervation: Nn. spinales 2, 3, and 4.

Trunco-stelepodial—Dorsal

LATISSIMUS DORSI

This muscle consists of a large, superficial fanshaped sheet. It opposes the action of the trapezius, cephalo-clavicularis and cleido-humeralis.

Origin: From the fascia of the dorsal midline from the level of the eighth to the level of the fifteenth vertebræ its fibers extend ventro-anteriorly, its fibers converging toward their

Insertion: It passes between the scapular and coracoid heads of the anconeus medius to insert on the postero-dorsal surface of the head of the humerus.

Action: Abductor and retractor of the femur.

Innervation: Nn. spinales 8 to 15.

Trunco-stelepodial—Ventral

PECTORALIS

This muscle is a very powerful adductor of the humerus. Its anterior portion draws the humerus forward, acting independently, while the posterior fibers draw the humerus backward.

Origin: From the posterior border of the episternum and the medial portion of the clavicle, from the medial border of the coracoid, and by digitations from the anterior fifteen gastralea.

Insertion: On the ventral portion of the head and adjacent proximal portion of the humerus.

Innervation: Nn. spinales 7 to 10.

Zono-stelepodial—Dorsal

DORSALIS SCAPULÆ

Origin: From the lateral surface of the dorsal third of the scapula its fibers converge ventrally to their

Insertion: On the anterior surface of the head of the humerus, dorsal to the insertion of the cleido-humeralis.

Action: Abductor of the humerus.

Innervation: N. spinalis 6.

EPICORACO-HUMERALIS

Origin: From the dorsal (inner) surface of the coracoid, it curves posteriorly around that bone to its

Insertion: On the posterior surface of the proximal end of the humerus.

Action: Retractor of the humerus.

Innervation: Nn. spinales 6 and 7.

SCAPULO-HUMERALIS ANTERIOR

Origin: From the lateral surface of the scapula, beneath the dorsalis scapulæ.

Insertion: On the posterior border of the head of the humerus just lateral to the insertion of the scapulo-humeralis posterior.

Action: Rotator of the humerus.

Innervation: Nn. spinales 7 and 8.

SCAPULO-HUMERALIS POSTERIOR

Origin: From the posterior border of the scapula, its fibers extend ventrally to their

Insertion: On the posterior border of the head of the humerus.

Action: Rotator of the humerus.

Innervation: Nn. spinales 7 and 8.

SUBSCAPULO-CORACO-BRACHIALIS

Origin: From the posterior two-thirds of the mesial surface of the scapula, it passes laterally between the scapula and the first complete rib to its

Insertion: On the posterior border of the proximal portion of the humerus, ventral to the insertions of the scapulo-humeralis anterior and posterior.

Action: Rotator of the humerus.

Innervation: N. spinalis 8.

CLEIDO-HUMERALIS

Origin: From the posterior border of the lateral four-fifths of the clavicle, it extends posteriorly to its

Insertion: On the anterior border of the head of the humerus and a slip which gives rise to the humero-radialis.

Action: Protractor of the humerus.

Innervation: N. spinalis 7.

Zono-stelepodial—Ventral

CORACO-BRACHIALIS BREVIS

This is a very small but distinct slip of the coraco-brachialis which lies between the anterior portion of the pectoralis and the coraco-brachialis medius. It aids in adduction of the brachium.

Origin: From the anterior portion of the medial border of the coracoid, it passes laterally to its

Insertion: On the ventral surface of the head of the humerus mesiad from the insertion of the pectoralis.

Innervation: Nn. spinales 6 and 7.

CORACO-BRACHIALIS MEDIUS

This muscle comprises the anterior portion of the coraco-brachialis mass; it is separated from the coraco-brachialis longus by the ventral nerve trunk to the antibrachium.

Origin: From the anterior half of the ventral surface of the coracoid it extends laterally to its

Insertion: On the ventral surface of the head of the humerus and the proximal portion of its posterior surface.

Action: Adductor and retractor of the humerus.

Innervation: Nn. spinales 6 and 7.

CORACO-BRACHIALIS LONGUS

This muscle comprises the posterior moiety of the coraco-brachialis mass. Together with muscle just described, the coraco-brachialis longus and the pectoralis are the chief mechanical agencies used in raising the anterior portion of the body from the ground. Because of the poor adjustment of the limbs for walking—they are still truly 'lateral' appendages and sprawl badly—this group of muscles is necessarily very heavy.

Origin: From the posterior half of the ventral surface of the coracoid, it extends laterally to its

Insertion: Along the distal two-thirds of the posterior border of the humerus.

Innervation: Nn. spinales 7 to 10.

SUPRACORACO-HUMERALIS

This muscle is continuous at its origin with the coraco-brachialis medius but separates from that muscle to pass dorsad to the head of the humerus.

Origin: From the dorsal portion of the anterior border of the coracoid, it passes beneath the cleido-humeralis and dorsal to the head of the humerus to its

Insertion: On the posterior border of the proximal portion of the humerus, just lateral to the insertion of the scapulo-humeralis anterior.

Action: Rotator of the humerus.

Innervation: N. spinalis 8.

Zono-zeugopodial—Dorsal

ANCONEUS MEDIALIS

Origin: By a tendon from the ventro-caudal portion of the lateral surface of the scapula and by a second tendon from the posterior border of the coracoid. These tendons unite and become muscular just lateral to the latissimus dorsi, which passes between them, and become muscular. The tendon from the scapula receives an accessory tendon which passes to it from the humerus beside the anterior border of the latissimus dorsi. Its fibers extend laterally to their

Insertion: In common with the other two portions of the anconeus group, on the olecranon process of the ulna.

Zono-zeugopodial—Ventral

CORACO-ANTIBRACHIALIS

Origin: From the third fourth posterior of the coracoid, it passes laterally, narrowing to a thin flat ligament as it passes the head of the humerus, and finally passes between the coraco-brachialis longus and the humero-antibrachialis to its

Insertion: On the proximal portion of the medial border of the radius.

Action: Flexor of the antibrachium.

Innervation: Nn. spinales 6, 7, and 8.

Stele-zeugopodial—Dorsal

HUMERO-RADIALIS

Origin: From the lateral portion of the cleido-humeralis, whence it extends laterally to its

Insertion: On the proximal portion of the medial surface of the radius.

Action: It is a flexor of the antibrachium.

Innervation: N. spinalis 7.

ANCONEUS LATERALIS

Origin: From the lateral surface of the head of the humerus, just caudal to the insertions of the cleido-humeralis and of the dorsalis scapulæ, it extends laterally between the humero-radialis and the anconeus medialis, unites with the latter and passes to its

Insertion: On the olecranon process by the aponeurosis common to the group.

Action: Extensor of the antibrachium.

Innervation: Nn. spinales 7 and 8.

ANCONIUS BREVIS

Origin: From the posterior border of the humerus, beneath the anconeus medialis. It is a small muscle lying just dorsal to the coraco-brachialis longus and passes laterally from its origin to its

Insertion: In common with the anconeus medialis and the anconeus lateralis, on the olecranon process.

Innervation: Nn. spinales 7 and 8.

Zono-zeugopodial—Ventral

HUMERO-ANTIBRACHIALIS

Origin: From the proximal portion of the antero-ventral surface of the humerus just distal to the insertion of the pectoralis.

Insertion: On the proximal portion of the ventro-mesial surface of the radius.

Action: Flexor of the antibrachium.

Innervation: Nn. spinales 6, 7, and 8.

PRONATOR TERES

Origin: From the anterior surface of the medial condyle of the humerus it extends laterally and anteriorly beneath the flexor carpi radialis to its

Insertion: On the ventro-mesial surface of the distal half of the radius.

Action: Pronator of the antibrachium.

Innervation: N. spinalis 6.

Stele-actinopodial—Dorsal

EXTENSOR CARPI RADIALIS

Origin: From the anterior surface of the outer condyle of the humerus it extends along the outer surface of the radius to its

Insertion: For the most part, by muscle fibers on the outer surface of the distal portion of the radius; a slip inserts by tendinous fibers on carpale 1.

Action: Extensor of the carpus and adductor of the antibrachium.

Innervation: N. spinalis 7.

EXTENSOR CARPI ULNARIS

Origin: From the outer condyle of the humerus, just distal to the origin of the extensor communis digitorum.

Insertion: Outer surface of carpale 5.

Action: Extensor of the carpus, abductor of the antibrachium.

Innervation: Nn. spinales 6, 7, and 8.

Zeugo-phalangopodial—Dorsal

SUPINATOR BREVIS

Origin: From the medial surface of the middle third of the ulna, its fibers run antero-distad to their

Insertion: On the base of the inner surface of the first metacarpal.

Action: Supinator of the manus.

Innervation: N. spinalis 7.

Interzeugopodial

PRONATOR QUADRATUS

Origin: From the inner surface of the distal two-thirds of the ulna its fibers traverse the space between the radius and the ulna to their

Insertion: On the inner surface of the distal head of the radius.

Action: Pronator of the antibrachium.

Innervation: Nn. spinales 6, 7 and 8, ventral.

Stele-actinopodial—Ventral

FLEXOR CARPI RADIALIS

Origin: From the medial condyle of the humerus, its fibers extend distad and diagonally across the antibrachium to their

Insertion: On the lateral surface of the base of the first metacarpal

Action: Flexor of the manus.

Innervation: Nn. spinales 6 and 7.

FLEXOR CARPI ULNARIS

Origin: From the inner surface of the medial condyle of the humerus, it extends along the outer border of the ulna to its

Insertion: On the outer surface of carpale 5.

Action: Flexor of the carpus and abductor of the manus.

Stele phalangopodial—Dorsal

EXTENSOR COMMUNIS DIGITORUM

Origin: From the lateral condyle of the humerus, it extends superficially to its

Insertion: Into the aponeurosis covering the dorsum of the manus and on the dorsal surfaces of the distal series of carpals.

Action: Levator of the manus and extensor of the antibrachium.
Innervation: Nn. spinales 7 and 8.

FLEXOR COMMUNIS DIGITORUM

Origin: 1) By one head from the medial condyle of the humerus; 2) a second head from the proximal half of the ulna; 3) a small lateral head from the distal portion of the ventral surface of the ulna.

Insertion: This muscle broadens into a flat tendinous sheet which divides into five tendons which are inserted into the bases of the ultimate phalanges of each of the digits.

Action: Flexor of the phalanges.

Innervation: Nn. spinales 7 and 8.

Basi-phalangopodial—Dorsal

EXTENSORES COMMUNIS DIGITORUM BREVES

a) Adductor pollicis brevis

Origin: The muscles comprising the group have a common origin on the distal portion of the dorsal surface of the ulna. The adductor pollicis brevis is the first slip of the group.

Insertion: On the inner surface of the first phalanx of the first digit.

b) Extensor pollicis brevis

This is the second slip of the group.

Insertion: On the ultimate phalanx of the first digit.

c) Extensores communis digitorum breves

The slips to the four remaining digits have been grouped under this head as no abductor minimi digiti has been differentiated.

Insertion: On the ultimate phalanges of digits two to five.

Action: This group of muscle slips furnishes the chief means for extension of the digits.

Innervation: N. spinalis 7.

Basi-phalangopodial—Ventral

FLEXORES COMMUNIS DIGITORUM

Origin: By a head from the distal portion of the ventral surface of the ulna and by a head from the flexor communis digitorum.

Insertion: This sheet is perforated near the points of insertion by the tendons of the flexor communis digitorum and thus has a point of insertion on both sides of each of the phalanges of the proximal series.

Action: Flexor of the digits.

Innervation: Nn. spinales 6, 7, and 8.

LUMBRICALES

Origin: These muscles, six in number, take origin from the ventral surface of the tendinous distal portion of the flexor communis digitorum.

Insertion: On the lateral surfaces of the proximal phalanges of digits two, three, and four.

ADDUCTORES COMMUNIS

Origin: From the ventral surface of the ulnare, this sheet extends antero-dorsad to its

Insertion: On the ventral surface of the proximal phalanges of digits one, two, and three.

Action: Adductor and pronator of the manus.

Innervation: Nn. spinales 6, 7, and 8.

FLEXOR POLLICIS

Origin: From the ventral surface of carpale 1.

Insertion: On the base of the proximal phalanx of the first digit.

ABDUCTOR POLLICIS

Origin: From the ventral surface of the intermediale.

Insertion: On the medial surface of the proximal phalanx of the first digit.

Action: Abductor of the pollex.

ABDUCTOR DIGITI MINIMI

Origin: From the ventral surface of carpale 4.

Insertion: On the inner surface of the proximal phalanx of the fifth digit.

OPPONENS DIGITI MINIMI

Origin: From the lateral surface of the ulnar sesamoid.

Insertion: On the ventral surface of the proximal phalanx of the fifth digit.

Actino-phalangopodial—Dorsal

INTEROSSEI DORSALES

Origin: From the bases of all the metacarpals.

Insertion: On the dorsal and lateral surfaces of the bases of the proximal series of phalanges.

Actino-phalangopodial—Ventral

INTEROSSEI VOLARES

Origin: From the ventral surfaces of the bases of the metacarpals.

Insertion: On the ventral and inner surfaces of the bases of the proximal series of phalanges.

Action: Both series of interossei act as abductors and adductors of the digits.

Innervation: All the deep muscles of the hand are innervated by nn. spinales 7 and 8.

Posterior Limb

Trunco-zonal—Ventral

CAUDI-FEMORALIS

Origin: From the lateral surfaces of the hæmal spines of the caudal vertebræ, its fibers extend antero-laterally to their

Insertion: The fibers of this muscle converge and pass between the ilium, the ischium, and the tendinous portion of the caudi-ischio-tibialis to insert on the proximal portion of the ventral surface of the femur. An accessory tendon arises on the lateral surface of the muscle near the point of insertion and runs laterally, parallel to the femur, to insert on the proximal portion of the medial surface of the tibia.

Action: This muscle serves a three-fold function; it is a rotator of the femur, adductor of the femur and an abductor-adductor of the tail. By means of its accessory ligament to the tibia, it also aids in tensing the leg.

Innervation: Nn. spinales 27 and caudal.

CAUDI-ISCHIO-TIBIALIS

Origin: From the ventral surfaces of the transverse processes of the six anterior caudal vertebræ and from the tuber ischium.

Insertion: On the proximal portion of the medial surface of the tibia.

Action: Flexor of the crus on the shank.

Innervation: Nn. spinales 26, 27, and caudal.

ISCHIO-CAUDALIS

Origin: From the lateral surfaces of the hæmal spines of the caudal vertebræ.

Insertion: On the tuber ischium.

Action: Depressor and abductor-adductor of the caudal region.

Innervation: N. spinalis 27 and the succeeding caudal nerves.

Zono-stelepodial—Dorsal

ILIO-FEMORALIS

Origin: From the dorsal portion of the lateral surface of the ilium.

Insertion: On the middle third of the caudal surface of the femur.

Action: Abductor and rotator of the femur.

Innervation: N. spinalis 24.

ISCHIO-TROCHANTERICUS

Origin: From the caudal portion of the inner surface of the ischium, it curves around the posterior border of the ischium and then runs anteriorly to its

Insertion: On the posterior surface of the inner trochanter.

Action: Rotator of the thigh.

Innervation: Nn. spinales 25 and 26.

PUBO-ISCHIO-FEMORALIS INTERNUS

Origin: From the inner surface of the pubis and from the anterior portion of the inner surface of the ischium, this muscle curves antero-dorsally around the anterior side of the pubis just lateral to the pubic tuberosity, to its

Insertion: On the second proximal fourth of the dorso-anterior surface of the femur, along the anterior border of the origin of the femoro-tibialis.

Action: Extensor and rotator of the femur.

Innervation: N. spinalis 23.

Zono-stelepodial—Ventral

PUBO-ISCHIO-TROCHANTERICUS

Origin: From the entire ventral surface of the pubo-ischiadic plate its fibers extend laterally to converge at their

Insertion: On the ventral surface of the inner trochanter of the femur.

Action: Adductor of the thigh.

Innervation: N. spinalis 24.

PUBO-FEMORALIS

Origin: From the inner surface of the pubis and the lateral pubic tuberosity, this muscle extends laterally between the femoro-tibialis which lies dorsal to it and the pubo-tibialis which lies ventral to it, to its

Insertion: On the middle portion of the ventro-caudal surface of the femur.

Action: Abductor and rotator of the femur.

Innervation: N. spinalis 24.

ISCHIO-FEMORALIS

Origin: From the middle proximal portion of the dorsal surface of the pubo-ischio-tibialis and it extends into the thigh parallel to that muscle.

Insertion: On the ventral surface of the femur, lateral to the insertion of the pubo-femoralis.

Action: Adductor of the thigh.

Innervation: Nn. spinales 26 and 25.

Zono-zeugopodial—Dorsal

EXTENSOR ILIO-TIBIALIS

Origin: From the dorsal half of the anterior border of the ilium.

Insertion: On the proximal portion of the anterior surface of the tibia.

Action: Extensor of the crus.

Innervation: N. spinalis 24.

AMBIENS

Origin: By tendinous fibers from the lateral tuberosity of the pubis.

Insertion: On the proximal portion of the anterior surface of the tibia.

Action: Extensor of the crus.

Innervation: N. spinalis 24.

Remarks: The two preceding muscles have a common insertion and have been termed the extensor triceps femoris.

ILIO-FIBULARIS

Origin: From the posterior border of the ilium, just above the level of the acetabulum.

Insertion: On the lateral surface of the proximal end of the fibula.

Action: Flexor of the crus.

Innervation: N. spinalis 25.

Remarks: This muscle has been termed the biceps femoralis by Furbringer and since it is quite certainly supplied by the nerve which is homologous with the peroneus communis of higher forms,

this homology may certainly be accepted. If this be true, however, the ilio-fibularis can in no case be serially homologous with the coraco-antibrachialis of the forelimb which has been termed the biceps brachii by Furbringer.

Zono-zeugopodial—Ventral

PUBO-ISCHIO-TIBIALIS

Origin: From the ventral surface of the lateral pubic tuberosity, from the ischiadic and pubic symphyses by a thin, tough, tendinous sheet; the separate elements of this sheet converge and thicken into a heavy, flat muscle which covers almost the entire ventral surface of the thigh.

Insertion: On the proximal portion of the ventral surface of the tibia.

Action: Flexor of the tibia; adductor of the entire leg.

Innervation: Nn. spinales 25 and 26.

PUBO-TIBIALIS

Origin: From the lateral surface of the lateral pubic tuberosity.

Insertion: On the proximal portion of the inner aspect of the tibia.

Action: Adductor and flexor of the crus.

Innervation: N. spinalis 24.

ISCHIO-TIBIALIS POSTICUS

Origin: From the lateral tuberosity of the ischium.

Insertion: On the medial aspect of the tibia, just distal to the insertion of the caudo-ischio-tibialis.

Action: Flexor of the crus.

Innervation: N. spinalis 24.

ISCHIO-TIBIALIS POSTICUS

Origin: From the lateral tuberosity of the ischium.

Insertion: On the medial aspect of the tibia, just distal to the insertion of the caudo-ischio-tibialis.

Action: Flexor of the crus.

Innervation: Nn. spinales 26 and 27.

Remarks: A slip arises from the distal end of this muscle and forms a part of the origin of the flexor communis digitorum.

FEMORO-TIBIALIS

Origin: From the middle third of the dorso-anterior surface of the femur.

Insertion: On the proximal portion of the antero-lateral surface of the tibia, in common with the ambiens and the extensor ilio-tibialis.

Action: Extensor of the crus.

Innervation: By the second nerve of the lumbar plexus.

Stele-phalangopodial—Dorsal

EXTENSOR COMMUNIS DIGITORUM

Origin: From the dorsal surface of the distal end of the femur, it extends superficially along the middle of the dorsal side of the crus to its

Insertion: On the inner surfaces of the bases of the third and fourth metatarsals; each of the two slips is continued as a tendon which runs along the inner surface of the third and fourth digits to insert on their penultimate phalanges.

Action: Levator of the pes and adductor of the third and fourth digits.

Innervation: N. spinalis 25.

Stele-phalangopodial—Ventral

FLEXOR COMMUNIS LONGUS DIGITORUM

Origin: From the medio-caudal surface of the femur, from the medial surface of the fibula, a head from the gastrocnemius and a head from the ischio-tibialis posticus.

Insertion: On the ultimate phalanges of each of the digits.

Action: Flexor of the digits.

Innervation: N. spinalis 26.

Stele-zeugopodial—Ventral

GASTROCNEMIUS

Origin: From the ventral surface of the distal end of the femur, from the fibula and a head from the ischio-tibialis posticus.

Insertion: Into the plantar aponeurosis.

Innervation: N. spinalis 26.

Zeugo-basipodial—Dorsal

TIBIALIS ANTICUS

Origin: From the proximal portion of the anterior surface of the tibia.

Insertion: On the lateral surface of the tibiale, continued forward as a tendon to the lateral surface of the first digit, terminating on the penultimate phalanx.

Action: Adductor of the pes and of the first digit.

Innervation: Nn. spinales 25 and 26.

PERONEUS

Origin: From the proximal portion of the lateral surface of the fibula.

Insertion: On the lateral surface of the fibulare and on the lateral surface of the penultimate phalanx of the fifth digit.

Action: Abductor of the pes and of the fifth digit.

Innervation: N. spinalis 25.

FIBULO-TARSALE 4

Found in one specimen.

Origin: Dorsal surface of the distal head of the fibula.

Insertion: Tarsale 4.

Action: Levator of the foot.

Innervation: N. spinalis 25.

Zeugo-basipodial—Ventral

TIBIALIS POSTICUS

Origin: From the head of the tibia and the ventral surface of the fibula.

Insertion: Latero-ventral surface of the first phalanx of the hallux, and on the tibiale.

Action: Abductor of the hallux and flexor of the pes.

Innervation: Nn. spinales 25 and 26.

Zeugo-phalangopodial—Dorsal

ABDUCTOR ET EXTENSOR HALLUCIS LONGUS

Origin: From the lateral surface of the third distal fourth of the fibula.

Insertion: 1) Extensor portion: On the extensor tendon of the hallux; 2) Abductor of the hallux: On the dorso-lateral surface of the base of the first phalanx of the hallux.

Innervation: N. spinalis 25.

Interzeugopodial

PRONATOR QUADRATUS

Origin: From the medial surface of the distal half of the tibia.

Insertion: Slightly distal to the point of origin, on the medial surface of the fibula.

Action: Rotator of the crus.

Innervation: Nn. spinales 25 and 26.

Basi-phalangopodial—Dorsal

EXTENSORES BREVES DIGITORUM

Origin: The first from the dorsal surface of the tibiale, the remaining three from the dorsal surface of the fibulare.

Insertion: On the extensor tendons of the first four digits.

Action: Extensors of the digits.

Innervation: N. spinalis 25.

ABDUCTOR ET EXTENSOR DIGITI MINIMI

Origin: From the dorsal surface of the fibulare.

Insertion: On the extensor tendon of the fifth digit and the dorsal interossei.

Action: Abductor and extensor of the fifth digit.

Innervation: N. spinalis 25.

Basi-phalangopodial—Ventral

FLEXORES BREVES DIGITORUM

Origin: From the dorsal surface of the plantar aponeurosis.

Insertion: On the bases of the proximal phalanges.

Action: Flexor of the pes.

Innervation: N. spinalis 26.

LUMBRICALES

Origin: From the ventral surface of the distal portion of the flexor communis digitorum.

Insertion: On the inner surfaces of the proximal phalanges of the second, third and fourth digits.

Action: Adductor of the second, third and fourth digits.

Innervation: Nn. spinales 25 and 26.

ADDUCTORES HALLUCIS ET SECUNDI

Origin: From the ventral surface of the fibulare, beneath mm. adductores communis.

Insertion: On the dorsal and lateral surfaces of the penultimate phalanges of the first and second digits.

Action: Abductors of the first and second digits.

Innervation: Third nerve of the lumbar plexus.

Actino-phalangopodial—Dorsal

INTEROSSEI DORSALES

Origin: From the inner surfaces of the bases of all the metatarsals.

Insertion: On the dorsal and lateral surfaces of the bases of the proximal row of phalanges.

Action: Abductor-adductors of the digits.

Innervation: N. spinalis 25.

Actino-phalangopodial—Ventral

INTEROSSEI PLANTARES

Origin: From the inner surfaces of the bases of the second, third, fourth, and fifth metatarsals.

Insertion: On the outer surfaces of the penultimate phalanges of the first, second, third, and fourth digits.

OPPONENS DIGITI MINIMI

Arises from the inner surface of the base of the fifth metatarsal and inserts on the inner surface of the penultimate phalanx of the fifth digit.

Innervation: N. spinalis 26.

ANAL AND COPULATORY MUSCLES

Due to the fact that one of the specimens dissected had a necrotic mass in the wall of cloaca, and that the alimentary canal of the second had been removed for another study, previous to the dissections for this paper, a thorough dissection of these muscles was impossible. Consequently, no figures were attempted. The following account by Gadow, taken from his "Remarks on the cloaca and on the copulatory organs of the Amniota,"⁹ is, as far as could be determined, correct. Unfortunately, he made no figures to show the arrangement of the muscles.

"*Hatteria* possesses a m. perinei s. transverso-analis like the Lizards; also a m. transversus medianus almost exactly like that described in the Crocodilia; its most superficial fibers are transformed into a distinct outermost sphincter, which, according to the shape of the anal opening, lies transversely and not longitudinally as in the Crocodilia.

"From the outside of the m. transversus medianus, and covered by the m. sphincter, starts on each side a broad but thin muscle, which runs back and attaches itself aponeurotically on the skin and on the fascia of the ischio-caudalis, behind the anus. It resembles a very similar pair of muscles in the Lizards.

"The odoriferous glands get a coating of striped muscle fibers from the m. transversus medianus."

⁹ Gadow, H., Phil. Trans. of the Roy. Soc., B 178, p. 12.

SERIAL HOMOLOGIES

Serial homologies are based in this paper, whenever it is possible, on nerve supply. In cases in which the nerve supply was doubtful or seemed unconvincing, an attempt was made to correlate them with the more primitive condition found in *Necturus* and through such a correlation to arrive at a definite conclusion regarding their serial homology.

Before any homology can be attempted, the musculature must be divided into visceral and parietal groups according to its embryonic derivation. The visceral musculature includes all the muscles developed from the hypomeres and is confined to the anterior region of the body; this includes the integumental musculature of *Sphenodon*. The parietal musculature includes all the axial and appendicular musculature. Most of the homologies correspond to those described in previous work on this and other forms and in such cases no discussion was considered necessary.

VISCERAL MUSCULATURE

This group consists of the highly modified remnants of the gill arch musculature of lower forms. In *Sphenodon* it consists of the m. intermandibularis, m. sphincter colli, m. sphincter dorsalis, m. cerato-hyoideus, m. stylohyoideus, m. mylohyoideus, m. temporo-massetericus, m. pterygoideus externus, m. pterygoideus internus, m. depressor mandibulæ, m. constrictor laryngeus and m. dilator laryngeus.

SERIAL HOMOLOGUES IN THE VISCERAL MUSCULATURE

Derivatives from the mm. Levatores arcuum

Innervation by

N. trigeminus

temporo-massetericus
pterygoideus externus
pterygoideus internus

N. facialis

depressor mandibulæ
stapedius (Osawa)

Derivatives from the Depressors

Innervation by

N. trigeminus

mylohyoideus

cerato-hyoideus

N. facialis

intermandibularis
sphincter colli
sphincter dorsalis
stylohyoideus

N. vagus

constrictor laryngeus
dilator laryngeus

Judging from its position and relations, and by the process of elimination, the cerato-hyoideus must represent the anterior belly of the digastric of higher forms. Stretched as it is between two elements of the hyoid, and lying between the pterygoideus internus and the hyoglossus, its position is almost exactly that of the anterior belly of the digastric. Then, too, the remaining muscles of the hyoid of *Sphenodon* are constant or fairly so, through the higher forms while this muscle disappears entirely. Its innervation is that of the mylohyoid and the anterior intermandibularis of lower forms, the hypothetical phylogenetic precursor of the anterior belly of the digastric.

SERIAL HOMOLOGUES IN THE PARIETAL MUSCULATURE

Axial Musculature

Innervation by

Rami dorsales of nn. spinales

semispinalis capitis	sacro-transverso-transversalis interspinales
cervicis capitis	caudæ dorsalis
obliquus capitis	sacro-transverso-transversalis
rectus capitis posticus	

Rami ventrales of nn. spinales

Geniohyoideus, cleido-episterno-hyoideus, sterno-coracoideus profundus, rectus abdominis externus, ischio-caudalis (*partim*).

This, the most ventral series of axial muscles, is practically continuous from the symphysis menti to the caudal extremity. The geniohyoid is innervated by the hypoglossal nerve but that nerve is essentially a spinal nerve in function and phylogeny. The inclusion of the sterno-coracoideus profundus in this series might be questioned but since the coracoid and clavicle are movable, are moved, by this muscle, its internal position should not exclude it from the series.

Genioglossus, hyoglossus, sterno-coracoideus superficialis, rectus abdominis internus.

This second and deeper ventral series is not so complete as the more primitive superficial layer; it is broken in both the cervical and pelvic regions.

longus colli (<i>partim</i>)	ilio-sacro-costo-costalis	ilio-ischio-caudalis
longus colli (<i>partim</i>)	obliquus internus	ischio-caudi-tibialis
triangularis sterni	transversalis abdominis	

omohyoideus	
costo-coracoideus	intercostales interni longi
costo-sterno-coracoideus	
abdomino-costales	
intercostales interni breves	
intercostales externi breves	
trapezius	
latissimus dorsi (<i>partim</i>)	obliquus externus
levator scapulæ superficialis dorsalis	
cephalo-clavicularis	obliquus externus
serratus posterior (superficial layer)	
colli scapularis	uncini-costales breves
serratus anterior	uncini-costales longi
levator scapulæ ventralis superficialis	
serratus posterior (deeper portion)	intercostales externi longi
intercostales ventrales	costo-sterno-scapularis

The coccygeal portion of the caudi-ischio-femoralis and the ischio-caudalis (*partim*) are probably posteriorly the serial homologues of the above series, beginning with the omohyoideus.

SERIAL HOMOLOGY OF THE INTRINSIC MUSCLES OF LIMBS

Innervation by nn. spinales

6 and 7

24 and 25

Dorsal

cleido-humeralis	pubo-ischio-femoralis internus
latissimus dorsi (<i>partim</i>)	
dorsalis scapulæ	ilio-femoralis
scapulo-humeralis anterior	
scapulo-humeralis posterior	
humero-radialis	
supinator longus	ambiens

Ventral

supracoraco-humeralis	pubo-femoralis
coraco-brachialis brevis	ischio-femoralis
coraco-brachialis medius	pubo-ischio-trochantericus
subscapulo-coraco-humeralis	
epicoraco-humeralis	ischio-trochantericus.
6, 7, 8	25
anconeus lateralis	ilio-fibularis

The finding of satisfactory evidence for or against declaring the extensors and flexors of the forelimbs to be homologues of the extensors and flexors of the hind limbs has been difficult and has led to more or less disagreement among anatomists. Thane gives the following provisional homologies in the flexors of the proximal portions of the limbs in man; biceps flexor cubiti (innervation by the musculo-cutaneous nerve, C. 5 and 6) with the ischiadic head of the biceps cruris, the semitendinosus and the semimembranosus (innervation by the nerve to the hamstrings, L. 4 & 5, S. 1, 2, 3.); the humeral head of the biceps and the brachialis internus (innervation by the musculo-cutaneous) with the femoral head of the biceps cruris (innervation by the peroneal nerve, L. 5, S. 1, 2). Now Cunningham has propounded the following laws which he says are applicable to both fore and hind limbs: "The dorsal and ventral strata of muscles are always supplied by the corresponding dorsal and ventral branches of the nerves concerned—of two muscles, that nearer the head end of the body tends to be supplied by the higher nerve and that nearer the tail end of the body by the lower nerve." (Herringham)¹⁰

According to these laws, Thane's provisional homologies are impossible; but Thane makes exception to them as follows: "Nervous supply is undoubtedly the best and most valuable guide to muscular homology, but is however not infallible, since variations in the nerve supply occur sometimes in man, and muscles which undoubtedly correspond are occasionally supplied by different nerves in allied animals."¹¹ The innervation of these flexors and extensors, so far as can be ascertained, is constant throughout the limbed vertebrates from *Sphenodon* upwards, at least so far as the dorsal or ventral nature of their nerve supply is concerned, so Thane's exception would hardly seem to hold for them. His first homology, that of the biceps flexor cubiti with the three muscles of the hamstring group, may be correct though there would seem to be room for doubt because of the comparatively anterior innervation of the biceps flexor cubiti. But since it and its proposed homologues are all innervated by ventral branches, the homology may be correct, the discrepancy due to an elimination of the more posterior nerve fibers in an anterior shifting of the muscle.

As for the second homology, that of the humeral head of the biceps

¹⁰ Cunningham, D.J., Textbook of Anatomy, p. 671.

¹¹ Quain's Elements of Anatomy, Tenth ed., vol. 2, part 2, p. 277.

cubiti and the brachialis internus with the femoral head of the biceps cruris, that cannot hold. Even in man, as in the other limbed vertebrates possessing these muscles, the femoral head of the biceps is almost unique in its customary innervation by the common peroneal nerve, being the only muscle in the proximal portion of the hind limb to be regularly so supplied. In the anterior limb, the anconeus, (triceps) holds the same unique position as regards the musculo-spiral nerve, with the exception of a portion of the brachialis internus (and this far the proposed homology may be correct). Now the humeral head of the biceps cubiti is innervated by the musculo-cutaneous nerve, which is clearly a ventral nerve, and the femoral head of the biceps by n. peroneus communis, clearly a dorsal nerve. This dorsal character of the peroneus communis is exceptionally clear in *Sphenodon*. The peroneus communis is the sole source of nerve supply for the m. ilio-fibularis, which is certainly analogous in position, insertion and function with the femoral head of the biceps cruris of higher forms and, since its nerve supply is homologous with that of the femoral head of the biceps cruris of those higher forms, must be homologous with that muscle. Such a special homology has been proposed by Osawa and accepted by Gregory and Camp in their papers on osteology and myology.

The n. peroneus communis of *Sphenodon* is quite certainly serially homologous with the nerve of the anterior limb which supplies the m. anconeus since both are dorsal branches and the sole source of nerve supply for the superficial muscles of the distal portions of the limbs. For the same reasons, this anterior nerve must be accepted as the special homologue of the musculo-spiral of higher forms. Would it not then be reasonable to assume that, instead of the homology proposed by Thane, the m. anconeus lateralis and the m. ilio-fibularis should be serially homologous?

anconeus medius

extensor ilio-tibialis

anconeus brevis

femoro-tibialis

Innervation by nn. spinales

6, 7, 8

25, 26, 27

Ventral

pectoralis

caudi-femoralis

coraco-antibrachialis

pubo-ischio-tibialis

humero-antibrachialis

pubo-tibialis

coraco brachialis longus	ischio-tibialis posticus
flexor communis digitorum	caudi-ischio-tibialis
flexor carpi radialis	flexor communis dig. longus.
flexor carpi ulnaris	gastrocnemius
pronator teres	tibialis posticus (<i>partim</i>)
pronator quadratus	tibialis posticus (<i>partim</i>)
flexores breves digitorum	pronator quadratus
adductores communis	flexores breves digitorum
abductor pollicis	adductores communis
interossei volares	abductores communis
flexor pollicis	interossei plantares
apponens digiti minimi	tibialis posticus (distal portion)
adductor pollicis	flexores breves dig. (<i>partim</i>)

Dorsal

extensor carpi radialis	tibialis anticus
extensor carpi ulnaris	peroneus
supinator brevis	abductor et extensor hal. long.
extensor communis digitorum	extensor communis digitorum longus
extensor communis dig. breves	extensor pollicis brevis
abductor et ex. dig. min.	ex. com. dig. breves.
fibulo-tarsale 4	
interossei dorsales	interossei dorsales

DISCUSSION AND COMPARISON

While the musculature of *Sphenodon* is still very primitive in its nature, it shows some marked advances from the condition in the more primitive Urodeles. In discussing the advances found in the musculature of *Sphenodon*, the very excellent work of H. H. Wilder on the muscles of *Necturus* is used as a basis. *Necturus* presents the most primitive condition found in any of our living and familiar limbed vertebrates.

A brief survey would show a few major changes. Functional gills do not appear in *Sphenodon* and this fact with the elongation of the cervical region (it is longer by three segments) make a marked change in the musculature of that region. The greatest specialization in the muscular system of *Sphenodon* is shown in the axial

musculature and that of the distal portions of the limbs with the caudal musculature shows the least.

In making the special homologies necessary to such a comparison, the following points brought out by previous workers have been carefully heeded: that vertebrate parietal muscles are primarily divided into a group above the lateral line and a group or mass below the lateral line; that the limb muscles come from this ventral mass and that they too, are divided into a dorsal and a ventral mass; that the nerve supply is constant and split in the same way as the primary muscle masses; that these primary muscle masses may split longitudinally, transversely or horizontally to meet the needs of the stresses of varying habitat conditions that are important enough to make such splitting a survival character; that the units so produced may later fuse or disappear or shift their origins or insertions or both but that they seldom or never shift their nerve supply.

In the visceral musculature, there has been a considerable amount of shifting and restriction, due to the loss of the functional gills. The loss of the levatores arcuum and a corresponding spread of the posterior intermandibular, present the most striking superficial changes. The depressors of the most posterior gill arch have shifted to form the intrinsic muscles of the larynx and the anterior intermandibularis has given rise to the mylohyoideus and the coracohyoideus.

The disappearance of the gills has also led to a readjustment of the superficial axial muscles of the neck. The omohyoideus has shifted its insertion ventrally with the development of the hyoid apparatus. The trapezius has spread dorsally to the midline and anteriorly to the head; the cephalo-clavicularis is probably a product of the splitting of the trapezius. There have also been marked changes in the remainder of the axial musculature. The dorsal portion, which is without differentiation in *Necturus*, is split, except in the caudal region, into rather definite medial and lateral portions. Each of these longitudinal divisions has undergone a considerable amount of specialization which has been described in the body of this paper. The ventral axial musculature, which is also very simple in *Necturus*, has broken into a complex system of muscles for respiration and perhaps for crawling.

Proximal Portions of the Limbs

Anterior

Very few significant changes from the primitive condition have

taken place in this region. The procoraco-humeralis has disappeared or is present as the supracoraco-humeralis. An epicoraco-humeralis has developed from the ventral muscle mass and the brachio-radialis has split to form the humero-radialis and the supinator longus of *Sphenodon*. The coraco-brachialii have spread their origin to cover the entire ventral surface of the coracoid plate.

Posterior

The changes from the urodele condition shown in this region are not extensive. The pubo-ischio-tibialis has spread over the more anterior pubo-ischio-femoralis externus which in turn has split into the ischio-femoralis and the pubo-ischio-trochantericus. The pubo-tibialis has given rise to a m. pubo-femoralis and the pubo-ischio-femoralis to an ambiens. The rectus abdominis externus has extended posteriorly to the caudal border of the ischiadic plate. There has been a great increase in the extent but not in the number of the caudal muscles. The caudali-pubo-ischio-tibialis has split to form an ischio-tibialis posticus and the caudo-ischio-tibialis.

Distal Portions of the Limbs

Anterior

The dorsum of the antibrachium is quite like that of *Necturus*. There is, of course, an additional interosseous muscle and an additional short extensor for the first digit that which is not present in *Necturus*. The only other changes are a shift of the origin of the supinator to the medial surface of the ulna and the formation of an aponeurotic insertion for the extensor communis digitorum. The ventral surfaces show a single long flexor which inserts by tendons on the ultimate phalanges instead of into a palmar aponeurosis. A pronator teres appears, probably split from the flexor carpi radialis. The four layers of so-called flexors intrinsic to the foot¹² are still present. The only important changes they have made is that the flexor medius layer takes origin from the ventral surface of the long flexor tendon as the lumbricales, six in number, and the flexor profundus group is limited in its action to the three inner digits. Besides the typical fourth layer of interossei volares, there have split from the superficial flexor group an opponens digiti minimi, an abductor digiti minimi, an abductor pollicis and a flexor pollicis.

¹² McMurrich, J.P., Am. Journ. of Anat., vol. 6, p. 471.

Posterior

In the dorsum of the distal portion of the hind limb, the only noteworthy advances are the restriction of the insertion of the extensor communis digitorum to the third and fourth digits and the development of the abductor et extensor hallucis longus. Of the muscles in the ventral surface in this region, there is little to say. The long flexors have increased somewhat in extent and number of points of origin. The layers in the foot are quite like those in the hand except that there are only three lumbricales and that the third layer has split to form the adductores communis and abductores communis. Then, too, the opponens minimi digiti, abductor minimi digiti and abductor pollicis have no homologues, as separate entities in the foot. The flexor hallucis¹³ is a direct continuation of the tibialis posticus.

SUMMARY

1. Description of muscles: origin, insertion, action, and innervation have been given in tabular form for the sake of brevity; the figures are sufficient to illustrate the relations.

2. A distinct m. triangularis sterni was found; such a muscle has not previously been described in any animal lower than the class Aves.

3. The ventral axial musculature which has not previously been completely described or fully figured, has been completely discussed and illustrated.

4. Serial homologies have been made on a basis of innervation. An argument from facts brought to light by dissection and based on the most widely accepted laws for serial homology has been presented to prove the homology of the femoral head of the biceps cruris with the anconeus lateralis.

5. Diagrams of the complete innervation of both limbs have been included for greater clearness in the comparisons.

6. Special homologies of the muscles of *Necturus* with those of *Sphenodon*, with comparisons, have been made.

¹³ Osawa, G., Archiv. fur Mikros. Anat., Bd. 51.

BIBLIOGRAPHY

- Bardeen, C.R., The Nerves and Muscles of the Leg. *Am. Journ. of Anat.*, vol. 6, '06.
- Byerly, T.C., Note on the partial regeneration of the caudal region in *Sphenodon punctatum*. *Anat. Record*, vol. 30, '25.
- Cope, E.D., Origin of the Fittest. Appleton and Co., N.Y. '87, p. 234.
- Cunningham, D.J., Textbook of Anatomy, '06, p. 671.
- Ecker, A., Anatomy of the Frog. Trans. by G. Haslam, Oxford, '89, p. 182.
- Gadow, H., Remarks on the Cloaca and on the Copulatory Organs of the Amniota. *Phil. Trans. of the Roy. Soc., B* 178, '87. p. 12.
- Idem. Beitrage zur Morphologie der hinteren Extremitat der Reptilien. *Morph. Jahrbuch*, vol. 7, '82.
- Gegenbaur, C., Lehrbuch der Anatomie der Menschen, Leipzig, '96, Bd. 1, pp. 183 and 256.
- Gregory and Camp. Studies in Osteology and Myology. *Bul. of the Am. Mus. of Nat. Hist.*, vol. 38, '17, p. 437 *et seq.*
- Gunther, A., Contribution to the Anatomy of *Hatteria* (*Rhynchocephalus* Owen). *Phil. Trans. of the Roy. Soc.* 157, '67, p. 595 *et seq.*
- McMurrich, J.P., Phylogeny of the Plantar Musculature. *Am. Journ. of Anat.*, vol. 6, '06.
- Osawa, G., Beitrage zur Anatomie der *Hatteria punctata*. *Archiv. fur Mikros. Anat.*, Bd. 51, '98.
- Sobotta, J., Atlas and Textbook of Anatomy, ed. by McMurrich. Saunders Co., '09, p. 212.
- Thane, G.D., Quain's "Elements of Anatomy." Vol. 2, part 2. Tenth ed., London, '92, p. 277.
- Wiedersheim, R., Comparative Anatomy of Vertebrates, trans. by W.N. Parker, Macmillan, '97, pp. 128 and 140.
- Wilder, H.H., History of the Human Body. Holt & Co., N.Y., '09, pp. 189 *et seq.*

EXPLANATION OF FIGURES

1. Superficial muscles of the lateral aspect
2. Integumental muscles
3. Musculature of the dorsal aspect of the posterior limb
4. Ventral aspect of the anterior half of the body
5. Middle layer of the ventral muscles of the forelimb
6. Lateral aspect of the intercostal musculature
7. Medial aspect of the intercostal musculature
8. Ventro-internal aspect of the ventral axial muscles
9. Lateral aspect of the deeper muscles of the anterior region
10. Ventral aspect of the deeper muscles of the hyoid
11. Ventral aspect of the deep palmar muscles
12. Laryngeal muscles
13. Ventral aspect of the caudal half of the body
14. Ventral aspect of the deep muscles of the posterior limb
15. Fifth layer of muscles of the plantar aspect of the foot
16. Sixth layer of muscles of the plantar aspect of the foot
17. Seventh layer of muscles of the plantar aspect

NOMENCLATURE

A. m. ambiens. A.C. m. adductores communis. ACo. mm. abdomino-costales. ADM. m. abductor pollicis. AEDM. m. abductor et extensor digiti minimi. AL. m. anconeus lateralis. AM. m. anconeus medius. AP. m. adductor digiti minimi. APB. m. adductor pollicis brevis. CA. m. coraco-antibrachialis. CBB. m. coraco-brachialis brevis. CBL. m. coraco-brachialis longus. CBM. m. coraco-brachialis medius. CC. m. costo-coracoideus. CD. m. caudæ dorsalis. CEH. m. cleido-episterno-hyoideus. CF. m. caudi-femoralis. CH. m. cleido-humeralis. CHy. m. cerato-hyoideus. CL. m. constrictor laryngeus. CS. m. colli-scapularis. CSC. m. costo-sterno-coracoideus. DL. m. dilator laryngeus. DM. m. depressor mandibulae. DS. m. dorsalis scapulae. ECD. m. extensor communis digitorum. ECDB. m. extensor communis digitorum brevis. ECDL. m. extensor communis digitorum longus. ECR. m. extensor carpi radialis. ECU. m. extensor carpi ulnaris. EH. m. epicoraco-humeralis. EIT. m. extensor ilio-tibialis. FCDB. m. flexor communis digitorum brevis. FCDL. m. flexor communis digitorum longus (pedis). FCDs. m. flexor communis digitorum. FCR. m. flexor carpi radialis. FCU. m. flexor carpi ulnaris. FM. m. fibulo-tarsale 4. FP. m. opponens digiti minimi. FT. m. femoro-tibialis. G. m. gastrocnemius. GG. m. genioglossus. GH. m. geniohyoideus. HA. m. humero-antibrachialis. HG. m. hyoglossus. HR. m. humero-radialis. IC. m. ischio-caudalis. ICT. m. ischio-caudi-tibialis. IEB. mm. intercostales externi breves. IEL. mm. intercostales externi longi. IF. m. ilio-femoralis. IFi. m. ilio-fibularis. II. mm. intercostales interni breves. IIL. mm. intercostales interni longi. INT. m. intermandibularis. IPL. mm. interossei plantares. ISCC. m. ilio-sacro-costalis. IST. m. ilio-ischio-caudalis. ITP. m. ischio-tibialis posticus. IV. mm. intercostales ventrales. IVo. mm. interossei volares. L. mm. lumbricales. LC. m. longus colli. LSDS. M. levator scapulae dorsalis superficialis. LSVS. m. levator scapulae ventralis superficialis. M. m. mylohyoideus. OC. m. obliquus capitis. ODM. m. flexor pollicis. OE. m. obliquus externus. OH. m. omohyoideus. OI. m. obliquus internus. P. m. pectoralis. Pe. m. peroneus. PF. m. pubo-femoralis. PI. m. pterygoideus internus. PIT. m. pubo-ischio-tibialis. PT. m. pubo-tibialis. PITr. m. pubo-ischio-trochantericus. PT. m. pronator teres. RAI. m. rectus abdominis internus. RAE. m. rectus abdominis externus. RCP. m. rectus capitis posticus. S. m. supinator longus. SB. m. supinator brevis. SC. m. spinalis capitis. SeC. m. semispinalis capitis. SCP. m. sterno-coracoideus profundus. SCS. m. sterno-coracoideus superficialis. SH. m. stylohyoideus. SHA. m. scapulo-humeralis anterior. SP. m. scapulo-humeralis posterior. STT. m. sacro-transverso-transversalis. TA. m. tibialis anticus. TM. m. temporo-massetericus. TP. m. tibialis posticus. TrA. m. transversalis abdominis. TS. m. triangularis sterni. UCB. mm. uncino-costales breves. UCL. mm. uncino-costales longi.

PLATES



PLATE II

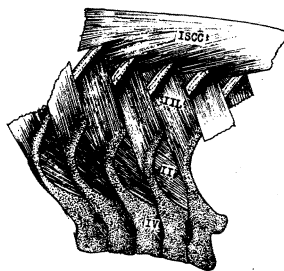
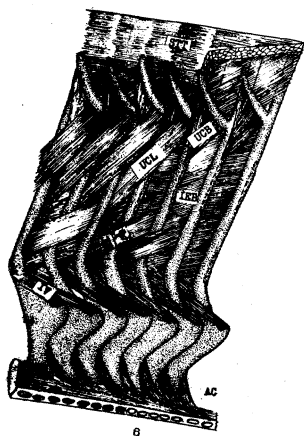
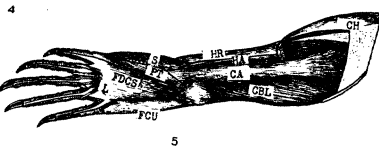
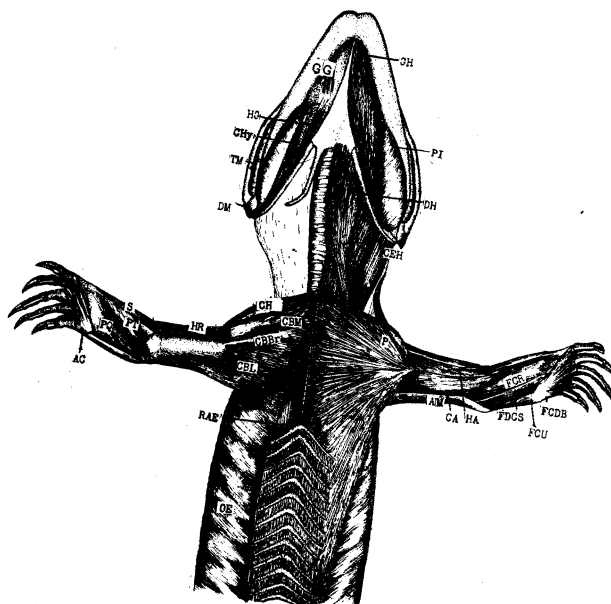
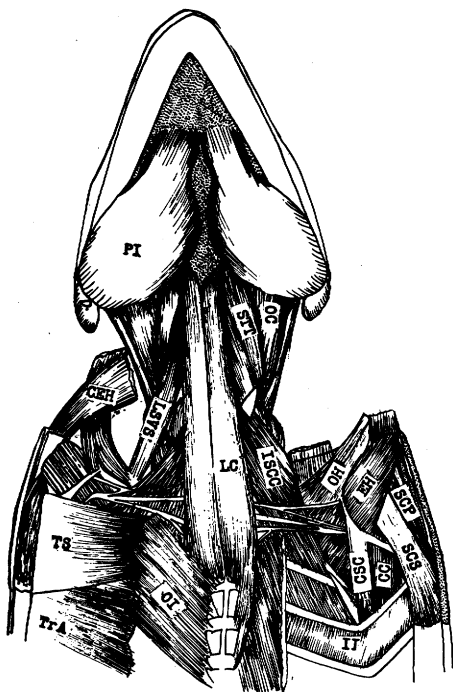
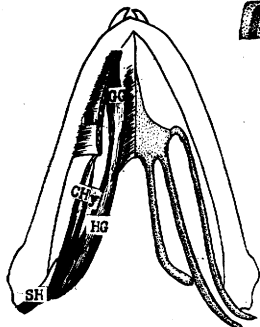


PLATE III



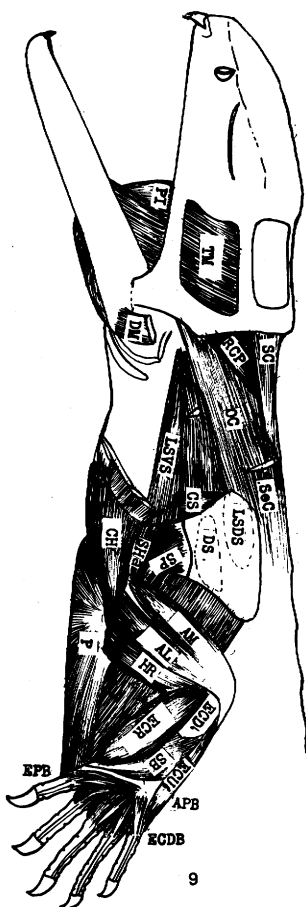
8



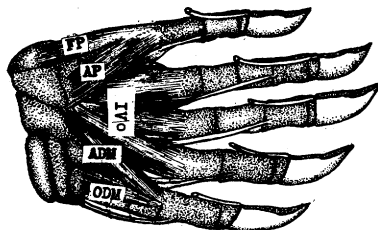
10



12

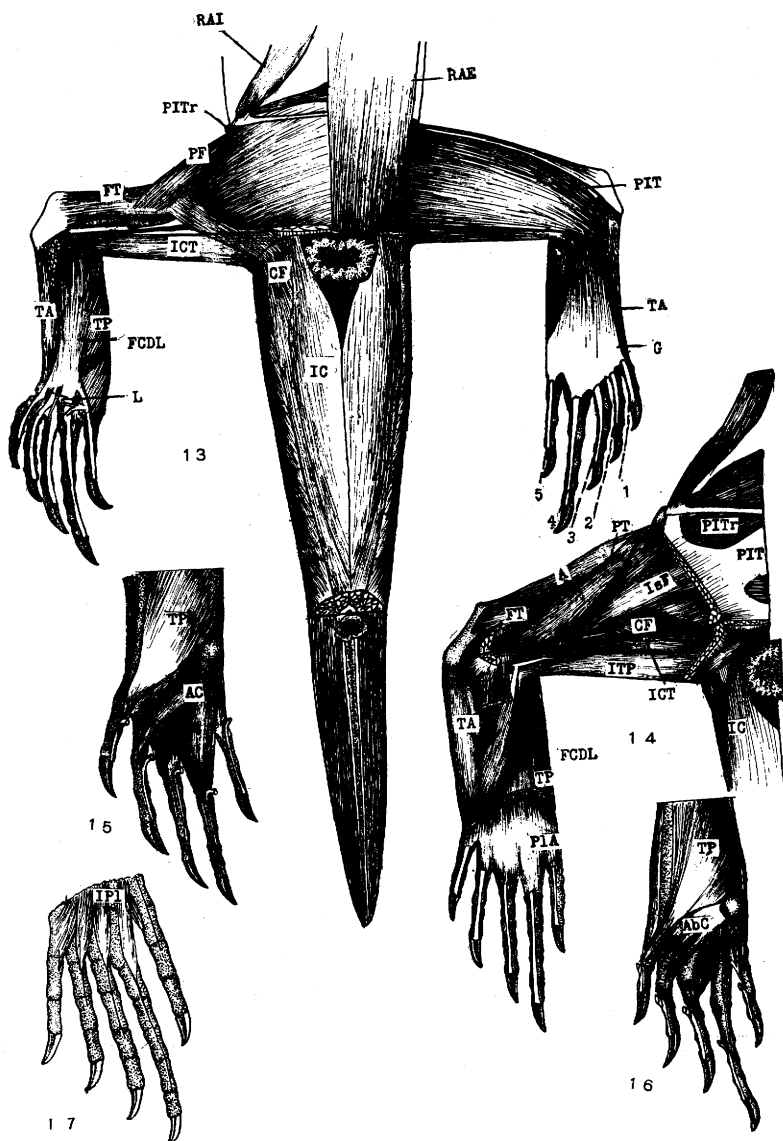


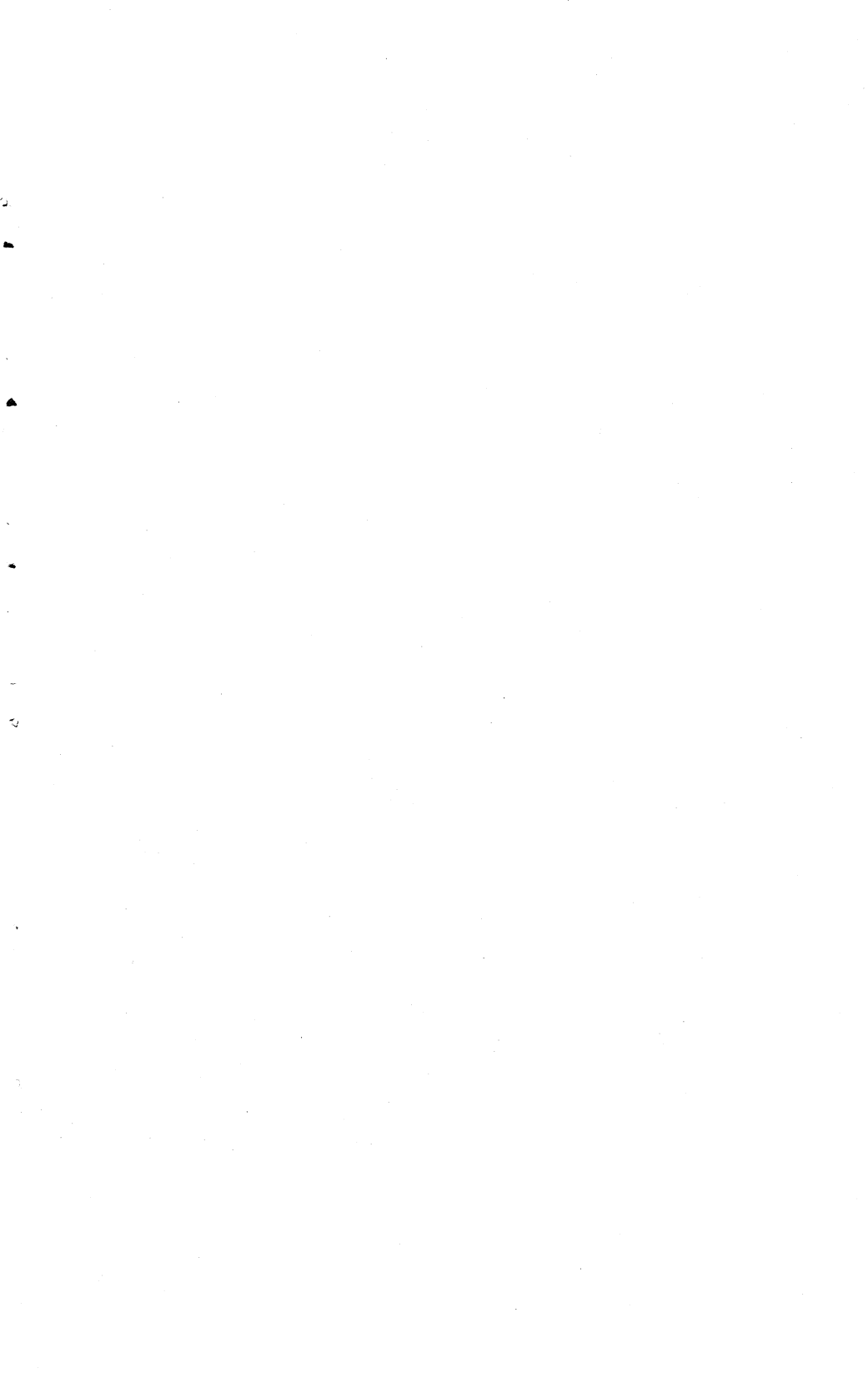
9



11

PLATE IV





UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

VOLUME XI

NUMBER 7

ECHINODERMS AND INSECTS FROM THE ANTILLES

PUBLISHED BY THE UNIVERSITY, IOWA CITY

CONTENTS

A New West Indian Cidarid

TH. MORTENSEN

*Report on the Holothurians Collected by the
Barbados-Antigua Expedition of the
University of Iowa in 1918*

ELISABETH DEICHMANN

*Lepidoptera Collected by the Barbados-Antigua
Expedition from the University
of Iowa in 1918*

A. W. LINDSEY

A NEW WEST INDIAN CIDARID

DR. TH. MORTENSEN
Zoological Museum, Copenhagen

In his "Report on the Crinoidea and Echinoidea collected by the Bahama Expedition from the University of Iowa in 1893" (Univ. of Iowa Monogr., 1, Ser. No. 15, Bull. Laborat. Nat. Hist., VII, p. 21) H. L. Clark mentions a specimen of *Histocidaris sharreri* taken "on the Pentacrinus ground off Havana." The specimen was not submitted to him for examination, only the photograph represented in Plate IV, fig. 1 of the said report, and the identification as *Histocidaris sharreri* is not due to him, having been made years ago in Washington, (probably by Rathbun). It did not fail to strike the attention of Clark that the specimen looked somewhat different from the typical *sharreri*; still he did not object to the identification as *Histocidaris sharreri*.

When making a closer study of the various species of *Histocidaris* for a Monograph of the Echinoidea under preparation I was struck by the very different aspect of the said specimen from the type of *Histocidaris sharreri*, as figured by A. Agassiz in the "Blake" Echini, Plate III, and could not help suggesting that it must be another species than *sharreri*. I then applied to Professor Nutting requesting him to do me the service of sending me some spines and pedicellariæ of the specimen. At the same time I asked my friend Professor H. L. Clark to send me a few spines and pedicellariæ of the typical *H. sharreri*, these having never been figured or described. Both Professor Nutting and H. L. Clark kindly complied with my wish, and I was thus able to make a direct comparison of the oral primaries and the pedicellariæ of the two specimens, and the result was that there proved to be so striking a difference in the shape of these structures, so very important from a classificatory point of view, that it was beyond doubt that they must represent two distinct species. Having reached this result I once more applied to Professor Nutting requesting him to supply me with information about the more important characters of the test of this specimen, which he very kindly did; moreover, he supplied me with a pair of fine photographs of the specimen. The additional information was decidedly

confirmatory of the result obtained from the study of the spines and pedicellariæ, and it must be regarded as an established fact that this specimen represents a new species of the genus *Histocidaris*, the second species of this genus recorded from the West Indies. The genus *Histocidaris* being very richly represented in the Pacific (—I have several new species from there—) its poor representation in the West Indian seas, *Histocidaris sharreri* being the only species hitherto known from there, is rather strange, and there is some satisfaction in the fact that a second, very well characterized species has now been proved to exist there. This also makes it reasonable to expect that still more interesting finds are awaiting us in those wonderfully rich West Indian seas.

The new species of which I shall here give a preliminary description accompanied by the photographs (—the full record to appear in the Monograph under preparation—) I take the pleasure of dedicating to Professor Nutting, naming it

Histocidaris nuttingi n. sp.

The specimen measures 60 mm. in horizontal diameter, nearly 50 mm. in height, apical system 28 mm. in diameter; the longest spine is 155 mm. long, thus 2.5 times the horizontal diameter. The ambulacra have the interporiferous area covered with numerous small spines, leaving no bare median area; this also holds good for the median interambulacral area. 9 interambulacral plates in a series. The ocular plates appear to be all in contact with the periproct, the two adjoining the madreporite only narrowly, the others broadly so. Genital pores very large, wholly inside the genital plates.

The *primary spines* are cylindrical, some of them slightly flaring and fluted at the tip. The surface of the shaft is smooth, with about 10 not very prominent longitudinal ridges, and some of them with sparsely distributed sharp, thorny spinelets. The collar is about 4 mm. long, distinctly thicker in the lower part. The oral primaries (three) are curved, elongate, slender, with very conspicuous serrations in the lower part, ending in a rather long non-serrate point (figs. 1-2). The *secondary spines* (fig. 4) are 8-9 mm. long, gently tapering to a rounded point; they are markedly concave in their whole length. The ambulacral spines are of the same length, but, as usual, much more slender, scarcely flattened. The *pedicellariæ* are very slender, the valves narrow, without any deepening in the blade above the apophysis (fig. 6). They reach a length of head of about 4 mm.; smaller samples do not differ in structure from the larger ones. It is a curious fact that the valves are often of unequal length (fig. 9); this may not improbably be due to their having broken off the point and then regenerated, though not to the original length. *Color* of both primary and secondary spines white, the collar only with a slightly darker tint.

Occurrence: Found on the "Pentacrinus ground" off Havana,

Morro Castle bearing S. W. by W. about two and one-half miles; 140 fathoms.

From *Histocidaris sharreri* the new species differs markedly in the shape of the spines and pedicellariæ. In *H. sharreri* the primary spines have numerous fine longitudinal ridges, finely and densely serrate; the oral primaries are short and broad, nearly spatulate, very different from the elegant, slender oral primaries of *H. nuttingi* (fig. 3). The ambital primaries are scarcely more than twice the horizontal diameter. The secondary spines are only slightly excavated in the middle and distinctly thickened at the end (fig. 5).

The pedicellariæ of the large form (fig. 10) have a broad, conical head; the blade is elongate-triangular, with sides somewhat re-enteringly curved, and with a conspicuous depression above the epiphysis (fig. 7). There is a small form of pedicellaria with narrow, slender valves (fig. 8), quite different from the larger form.

A good deal of confusion has been reigning with regard to *Histocidaris sharreri*, not only the new species here described, but also several other species having been confused with it. This was especially the case with *Calocidaris micans* (Mrtsn.), and I would take the opportunity here of calling attention to the fact that the Plate IV, figs. 1-2 of the "Blake" Echini, the only detail figures of "*Porocidaris sharreri*" ever published, are really of *Calocidaris micans*—as H. L. Clark on my suggestion has confirmed in a letter to me. Thus the only figure really representing *Histocidaris sharreri* is that on Plate III of the "Blake" Echini, which represents the type specimen of that species.

I beg to express my sincerest thanks to Professor C. C. Nutting and H. L. Clark for their kindness in supplying me with the necessary information and preparations, enabling me to establish the characters of the new species as well as of that rather ill-treated species, *Histocidaris sharreri*.

EXPLANATION OF FIGURES

Figs. 1-2. Oral primary spine of *Histocidaris nuttingi*, in front view (1) and side view (2). $\times 2.45$

Fig. 3. Oral primary spine of *H. sharreri*; front view. $\times 2.45$

Fig. 4. Secondary spine of *H. nuttingi*. $\times 12$

Fig. 5. Secondary spine of *H. sharreri*. $\times 12$

Fig. 6. Valve of large tridentate pedicellaria of *H. nuttingi*. $\times 27$

Fig. 7. Valve of large tridentate pedicellaria of *H. sharreri*. $\times 27$

Fig. 8. Valve of small tridentate pedicellaria of *H. sharreri*. $\times 27$

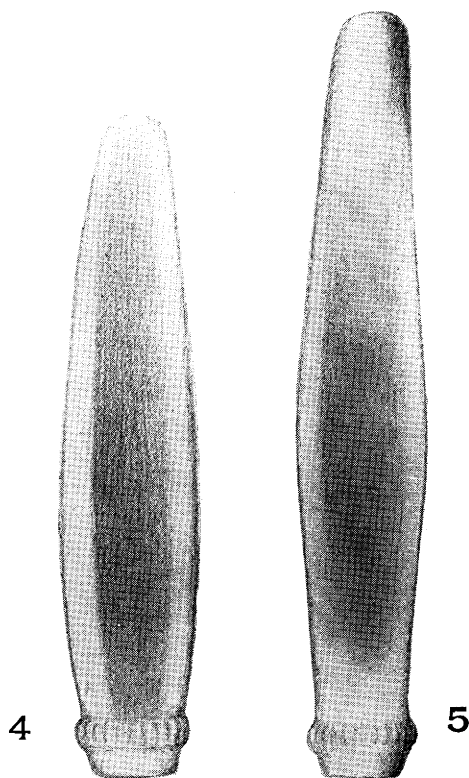
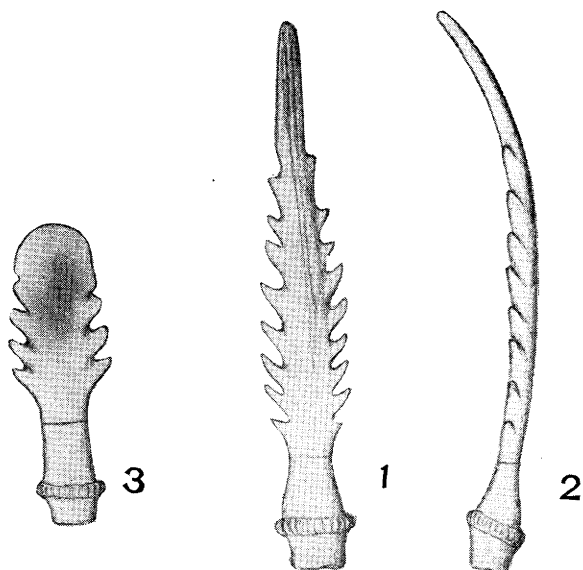
Fig. 9. Large tridentate pedicellaria of *H. nuttingi*. $\times 15$

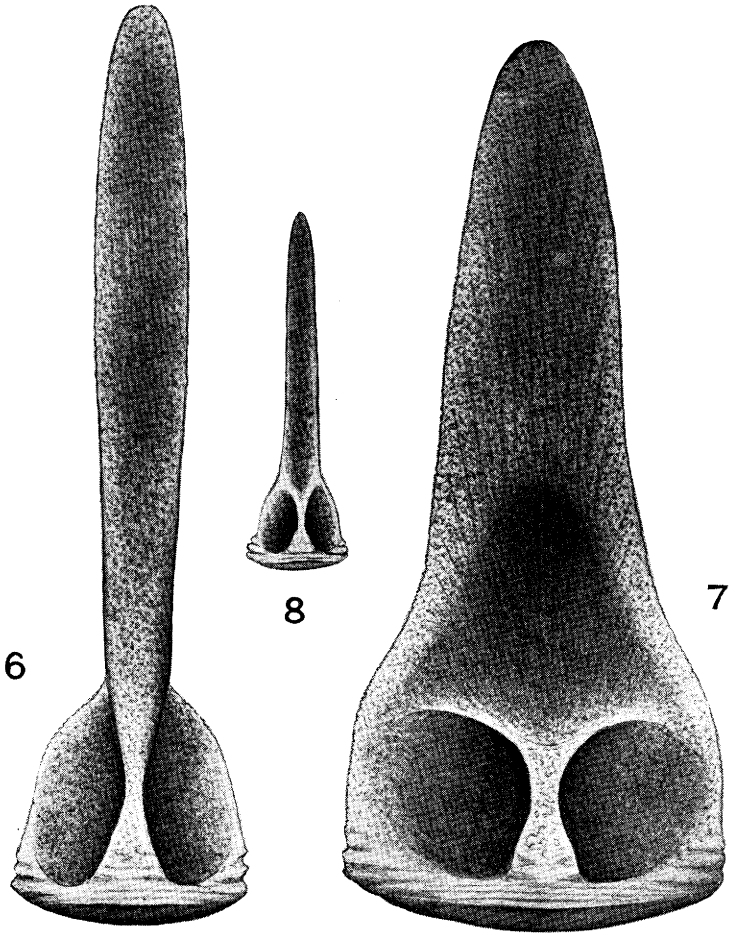
Fig. 10. Large tridentate pedicellaria of *H. sharreri*. $\times 15$

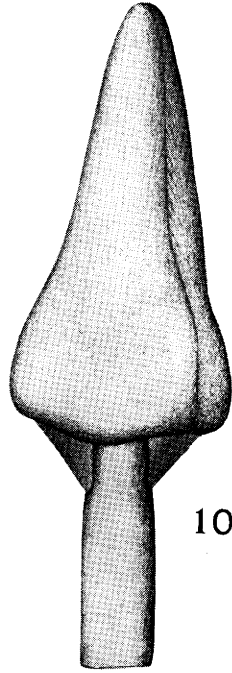
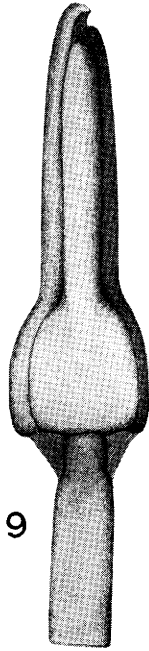
The stalk in figure 10 is drawn free hand, only an irregular fragment of a stalk being found in the preparations received from Prof. H. L. Clark.

Fig. 11. *Histocidaris nuttingi*, oral view

Fig. 12. *Histocidaris nuttingi*, aboral view







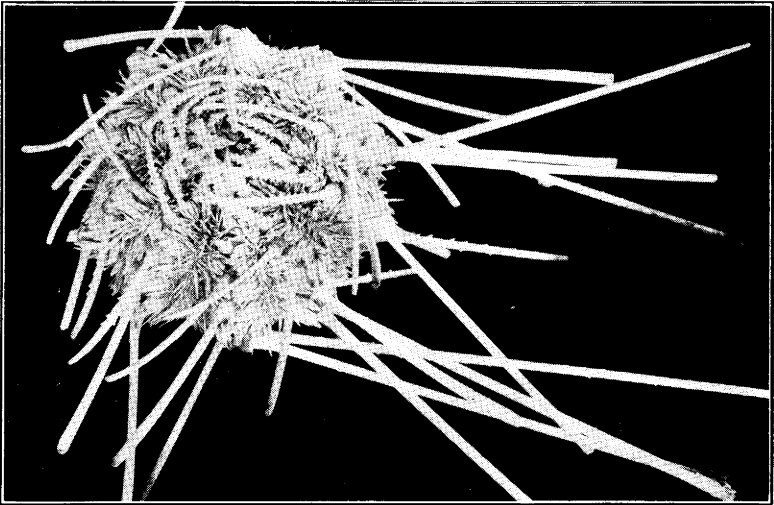


Figure 11

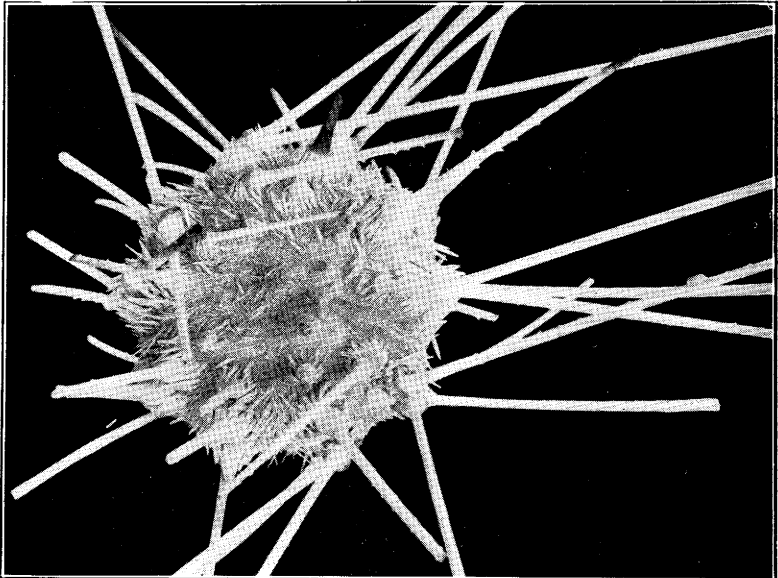


Figure 12

REPORT ON THE HOLOTHURIANS

Collected by the Barbados-Antigua Expedition from the
University of Iowa¹

ELISABETH DEICHMANN
Zoological Museum, Copenhagen

The collection of holothurians contains about 400 specimens divided among 18 species. All the West Indian species are represented except forms typical of the Florida Keys and the Greater Antilles. Sluiter's species are recorded for the first time since the types were secured. The apparently new species is a redescription, with a new name, of Selenka's well-known old species, *Stichopus rigidus*.

KEY TO WEST INDIAN HOLOTHURIANS

- a¹ Appendages present Actinopoda.
 - b¹ 20-25 peltate tentacles. Respiratory trees present; no retractor musculature. Holothuriidæ.
 - c¹ Tentacle ampullæ present, rete mirabile. Holothurinæ.
 - d¹ Genital organs in one tuft. Appendages scattered and not in distinct rows. Actinopyga.
 - Anal teeth present. Holothuria.
 - No anal teeth present. Holothuria.
 - d² Genital organs in two tufts; flattened forms with warts on the dorsal side. Usually C-shaped bodies among the deposits. Stichopus.
 - c² Tentacle ampullæ not present. Usually no rete mirabile. Synallactinæ.
 - Genital organs in single tuft. Mesothuria.
 - b² 10-20 dendroid tentacles present. No tentacle ampullæ. Retractor musculature present, respiratory trees present Cucumaridæ.

¹ Most of the specimens upon which this report is based were collected by the undersigned while a member of the Barbados-Antigua Expedition and are now in the collections of the State University of Iowa, Stanford University, and the California Academy of Sciences. I had originally intended, at Professor Nutting's request, to write the account of the Holothurians, and prepared the specimens with this end in view. Recently, however, Miss Deichmann has completed much preliminary (unpublished) work on the holothurians of the West Indies and has the group well in hand. It seems appropriate therefore that the report should embody the latest results. Miss Deichmann has, accordingly, relieved me of a rather difficult task. This paper is a contribution from the Hopkins Marine Station of Stanford University.

Certain ecological or field notes are interpolated in brackets and signed with my initials. W. K. Fisher.

- c¹ Appendages scattered over the surface of the body, very indistinctly in rows on the ambulacra.
 10 tentacles *Thyone*.
 16-20 tentacles *Phyllophorus*.
 a² No appendages, no respiratory trees *Paraetniodopa*.
 b¹ Deposits: Anchor and anchor plates. Tentacles pinnate.
Synaptinae.
 c¹ Anchors with smooth arms, vertex usually with knoblike projections.
 d¹ Stock of anchors branched irregularly. Calcareous ring without noticeable posterior prolongations. Stone canals not numerous. *Euapta*.
 Anchor longer than anchor plate; complicated rosettes are found scattered. *Euapta lappa* (J. Müller).
 d² Stock of anchor not branched. Tentacles 15 or fewer. Anchor plates rounded in front, narrow behind, with few holes, the largest dentate and regularly arranged. *Synaptula*.
 Normally 12 tentacles with 10-20 digits. Viviparous. Anchor as long as anchor plate. Small curved rods are found scattered. *Synaptula hydriformis* (Lesueur).
 b² Deposits: No anchors and no anchor plates. Tentacles peltato-digitate.
 Deposits: Six-spoked wheels. *Chiridotinae*.
 10-14 tentacles. Wheels collected in small papillae *Chiridota*.
 Numerous curved rods, with branched ends, scattered in the interambulacra. *Chiridota rotifera* Pourtales.

KEY TO THE SPECIES OF HOLOTHURIA

- a¹ Slender forms, without pronounced difference between dorsal and ventral side; tentacles small.
 b¹ Deposits: Tables and regular 6-holed buttons.
 c¹ Pedicels on distinct warts; skin rough to the touch. Genital organs fastened near the middle of the body. Cuvierian organs very large, transversely finely striated. Vascular ring near the calcareous ring. Tables regular, with 6 large holes in the brim, buttons with 6 large holes. *impatiens* (Forsk.)
 c² Pedicels not on distinct warts; skin smooth. Genital organs fastened near the vascular ring, which is unusually distant from the calcareous ring, (about 2 cm. in specimens 10-15 cm. long). Cuvierian organs small. Tables with 4 small holes in the corners of the disk or a complete ring of small holes; buttons with 6 holes varying from large to very small; buttons with numerous holes are often found. *arenicola* (Brandt).
 b² Deposits: Tables (usually with completely reduced disk) and den-

tate rods. Color dark reddish brown or more faded, usually two rows of dark spots on the dorsal side. Tentacles and pedicels yellow.

surinamensis Ludwig.

- a² Flattened forms, with fewer appendages on the dorsal side, often on warts, and numerous soft pedicels on the ventral.

b¹ Deposits: No tables, only scattered rods, with branched ends (never spinous). Uniform dark brown or pale brown; tentacles very large and bushy. *glaberrima* Selenka.

- b² Deposits: Tables, together with plates or buttons.

c¹ Tables high, simple, with small to rudimentary disk. Skin not stiff with spicules.

d¹ Perforated plates, biscuit-like with many small holes; some have larger holes, often only four, and they are more irregular. 20 tentacles; dorsal warts often indistinct. Color uniform dark with paler—reddish or pink—underside; space around base of pedicels dark (very small specimens 6 cm. long may be sand-colored). Stone canals numerous, in two tufts. Skin thick.

mexicana Ludwig.

d² Perforated plates with usually four larger central holes and often accessory holes in the brim; edge dentate. 20-25 tentacles. Dorsal warts generally very distinct, in longitudinal rows. Color in alcohol dark brownish and grey, sprinkled with small white dots, arranged in circles around the bases of the dorsal appendages. Color in life, Indian and ocher red above, with two rows of dark reddish brown spots and very numerous small dull green spots, sometimes forming a net design; ventral pedicels greenish yellow against dull Indian red. Stone canal single, well developed. *grisea* Selenka.

- c² Tables low, with large disk with knobbed brim and secondary rods, which unite with the spire so that the tables look as if they had numerous rods in the spire. Buttons strongly knobbed, with 6 holes in the dorsal buttons, 10 in the ventral; some few are flat. Supporting rods short and broad, with few holes. Skin stiff from spicules. Color in spirit dirty white. In life, sand color with two rows of dull brown mottlings above and often a rusty stain on ventral surface. Tentacles whitish, very small, and ventrally placed. *fossor* n.sp.

Holothuria impatiens (Forskaal)

Fistularia impatiens Forskaal, 1775, p. 121, pl. XXXIX, fig. B.

Holothuria botellus Selenka, 1867, p. 335.

Holothuria impatiens Lampert, 1885, p. 65 (complete list of references).—Theel, 1886, p. 233.—Fisher, 1907, p. 666, pl. LXIX fig. 4a.—Clark, 1901 b, p. 259; 1901, p. 494; 1919, p. 63.—Sluiter, 1910, p. 333.

The single specimen is typical and well developed in every respect.

This form seems never to be abundant; perhaps it lives below tide mark. Very few specimens are known from the West Indies and we know very little about its distribution. It has been taken from Tortugas, Porto Rico, and Tobago; not at Bermuda.

This species can not, for the present, be separated from the form which occurs in the Pacific Ocean, as Selenka already has pointed out.

1 specimen, English Harbor Point, Antigua, among small rocks.

Holothuria surinamensis Ludwig

Holothuria surinamensis Ludwig, 1874, p. 111, fig. 27.—Theel, 1886 a, p. 210; 1886 b, p. 7.—Heilprin, 1889, p. 136.—Clark, 1899, p. 133; 1901, p. 259; 1919, p. 63.—Verrill, 1907, p. 322.—Sluiter, 1910, p. 332.—Crozier, 1914, pp. 233-297; 1917, p. 560-566.

This form, (Plate 1, fig. 1,) which is known only from the West Indies, is very nearly related to *H. imitans* from Panama and Ludwig has regarded them as identical, while Theel keeps them separate. The tables are about twice as large as in *H. imitans*, which seems to be a rarer form, since few specimens are reported in any collection.

The shape of this species is very variable, ranging from strongly contracted, short specimens to completely extended forms. Further this form is able to multiply by fission (Crozier) and peculiar short forms with incomplete tentacle crown frequently occur. The color varies in alcohol from pale brownish to very dark and nearly all specimens have a double row of dark spots on their back. The deposits are so characteristic that no confusion is possible with other species known at present. An interesting fact is that in a very small specimen the tables have a well developed disk, which is very fragile and easily broken; the teeth on the top of the spire are also better developed in this young specimen and the rods with dentate edge are mostly developed with a series of holes along the edge.

The internal anatomy shows nothing peculiar and in most cases is difficult to study, as the animals often eviscerate themselves, or they are found in regenerating stages.

Ranges from Surinam, the type locality, to Bermuda.

130 specimens from Falmouth and English Harbor, Antigua; 2 from Barbados.

[This very abundant species at Antigua has two color phases which, so far as our observations extended, are characteristic of different habitats. A darker, more reddish or chocolate brown variety with pale brownish or brownish-pink, somewhat flesh-colored,

tentacles occurred at English Harbor, under rocks on the sheltered side of the Point, where a mauve-tinted, branching *Porites* was common.

The animals were sluggish and were living in such a way that the body was surrounded by stones, or stones and sand. At low tide they were always covered by a few inches of water, which on still days became very warm. In the laboratory two species of *Fierasfer* were recovered from the cloaca of some specimens being narcotized.

The other form, somewhat slenderer in habit and of a yellowish brown color, with yellow tentacles, was exceedingly common in Falmouth Harbor, in shallow water where it fairly swarms among corallines and under stones in the eel-grass area. It is found where the water has receded at low tide, and hence is very tolerant to heat and exposure. The shallow water in which they occur becomes very warm at mid-day and the animals are sometimes washed up on the beach or rolled around the edge, kept in motion by a ripple. They are always alive. They like very much an erect tufted or branched coralline, but are even commoner under rocks.

Owing perhaps to its tough constitution it is more difficult to kill with narcotizing reagents than other species of *Holothuria*. In life the animals are usually stained with a coating of fine silt or mud which adheres to their skin and partly obscures the rich brown coloring, upon which are marbling and spots of dark brown. The papillæ are rather prominent, unequal and pointed.

In aquaria they become restless, like the other variety.

—W. K. F.]

Holothuria arenicola Semper

Holothuria maculata Brandt, 1835, p. 46-47, (*Sporadipus*, subgenus *Acolhos*).—

Ludwig, 1881, p. 595; 1883, p. 156-157; 167-168.—Lampert, 1885, p. 73.—

Sluiter, 1910, p. 332.

Holothuria arenicola Semper, 1868, p. 61. pls. XX, XXX, fig. 13, XXXV, fig. 4.—Theel, 1886 a, p. 222.

Holothuria rathbuni Lampert, 1885, p. 73.—Theel, 1886 a, p. 268.—Clark, 1901 a, p. 343; 1901 b, p. 259, pl. XVII, fig. 7-10; 1919, p. 63.—Verrill, 1901, p. 37, fig. 6a-b, 7; 1907, p. 145, fig. 37.—Sluiter, 1910, p. 332.

This species is one of the commonest in the West Indies and cannot be confused with any other, as its outer appearance is so very characteristic, a long slender body, tapering toward both ends and small terminal tentacles. In the internal anatomy the unusually long distance of the vascular ring from the calcareous ring is the most remarkable feature.

The deposits are of the very common type, tables and 6-holed buttons. There is a very wide range of variation, in individual specimens as well as in the specimens from the same locality.

The tables have from 4 holes to a complete ring of holes in the disk; apparently the tables with only 4 holes are commonest in the larger specimens and they have a low spire, with single cross-beam, ending in few (8-12) teeth. Tables with higher spire are common in the small specimens and also found in the pedicels of the larger.

The 6-holed buttons have large or small holes; in the small specimens, where the buttons form only a thin layer, they are in nearly equal numbers; in the large specimens, where the buttons form the dominating layer, the small-holed are most numerous, but here also is variation; in some preparations not a single large-holed button can be found; in others it is difficult to say which kind is the commoner.

The supporting rods vary from simple ones, with few terminal holes and two larger on the middle (where they are broadest), to buttons with two rows of many small holes. The end plate seems to be the most constant deposit, with 6-10 larger holes in the middle, and a variable large number of smaller holes in the outer part.

This common form is known in two variations, one with small spots irregularly dotted over the body and one with two rows of large dark spots on the back. For the present these forms can be separated only by their coloration, but as they seem to occur in absolutely different localities, it will be natural to keep them separate, at least as varieties.

An interesting fact, which has long been known, is that these two forms occur in both the Pacific and the Atlantic Ocean. At least we are unable to find any differences, and the two varieties seem also to be restricted to different localities in the Pacific.

The type locality was the Bonin Islands where Brandt found the small spotted form (*H. maculata* Brandt). The same is common in the gulf of Panama and can not be distinguished from the specimens from the Atlantic side of Panama, or the specimens from Barbados.

Brandt's species was united with Semper's *H. arenicola* and as the name *maculata* is preoccupied by a *Synapta*, the name *arenicola* should be preferred; but both names have been used, without rule.

The name *rathbuni* was introduced by Lampert (1885) who named a species from Bahia secured by Rathbun. From the description given by Rathbun it is quite evident that it is *H. arenicola*, which

is known from this locality, the only difference being that Rathbun mentions a knobbed body, which doubtless originated from one of the species of *Thyone* which he examined from the same locality.

The name *rathbuni* was later applied to this species, first to the small spotted form, by Clark, 1901, who described and figured the spicules; and later also to the large spotted form by Verrill, 1904-07, who figured specimens from Bermuda. Sluiter, 1910, seems to use the name *rathbuni* only for the small spotted form, and says of *H. maculata*, which he also found, that he is unable to separate the West Indian from the Pacific specimens.

36 specimens from Pelican Isl. Barbados. 1 specimen from The Crane, E. Pt. Barbados. 17 specimens from English Harbor, Antigua. Common under rocks, entirely uncovered by low tide at Pelican Island, sluggish.

Holothuria grisea Selenka

Holothuria grisea Selenka, 1867, p. 328, pl. 18, fig. 251.—Semper, 1868, p. 92.

—Greef, 1882, p. 158.—Ludwig, 1882, p. 26.—Lampert, 1885, p. 85.—Theel, 1886, p. 214.—Clark, 1901, p. 258; 1919, p. 63.

Type locality, Haiti. This form, which seems never to be abundant, has a very wide range, nearly the same as that of *H. mexicana*, and is said to occur also on the west coast of Africa (Rolas, Greef, Z. Anz. Vol. V, No. 105, 1882). It is on the Atlantic side of Panama, along with *floridana* on the same coral rocks. At Florida it just touches the limit of *floridana*, but can hardly be said to belong to the fauna of Florida. It ranges as far south as Sao Paulo and Rio Janeiro.

The coloration of preserved specimens is very constant, being dark grey or brown, with small white spots arranged in rings around the bases of the dorsal appendages. These spots are the plates, which are accumulated in heaps in the skin. The dorsal warts are prominent and increase in number with advancing age. It has been supposed to be the young of *floridana* but can very easily be distinguished. The spicules are quite different and there is never, even in the largest specimen, more than one, free, well developed stone canal.

The present material indicates that the number of tentacles is not always 20, as Selenka observed, but varies to 23-25.

4 specimens from Falmouth Harbor, 2 from English Harbor, Antigua.

[The name *grisea* is a misnomer for this Harlequin of West Indian holothurians. All the specimens which I have seen are red in life with two rows of dark reddish brown spots along the back, which is peppered with dull green spots of small size, often in a reticulate design. The prominent lateral papillæ are usually lighter and brighter than the ground color of the back which is not uniform but is a marbling of Indian and ocher red, verging in places on dull orange vermillion. The ventral pedicels are greenish yellow against dull Indian red. Tentacles yellow with brown ends.

This form is found under rocks just below high tide, and is apparently nocturnal. It is usually soiled by mud so that it must be scrubbed to reveal the true colors. It was taken in eel-grass, at the surface of the sand and mud, English Harbor. It is very sluggish in the day time, especially when the tide is out, but at night, in aquaria, is active for a genus the members of which are not given to roving.—W. K. F.]

Holothuria mexicana Ludwig

Holothuria mexicana Ludwig, 1874, p. 101, fig. 47.—Lampert, 1885, p. 85.—

Theel, 1886, p. 215.—Clark, 1901 b, p. 258; 1919, p. 63.

Holothuria africana Theel, 1886, p. 174, pl. VIII, fig. 7.

Holothuria floridana Edwards, 1905, p. 383-384; 1908, p. 236-301.—Clark, 1919, p. 63.

The type locality is not known; the label was marked Mexico. It is the largest of the two West Indian holothurians, which are characterized by their numerous stone canals and deposits in form of tables and small plates or rosettes and it has been suggested that *mexicana* was the full grown form of *floridana* (Edwards, 1905, Science XXI, p. 383-384; and 1908, Biometrika, p. 236-301). The two forms are different. *H. floridana* has exclusively rosettes, while some few may have their branches united to form perforated plates resembling those of *mexicana*. *H. mexicana* has two kinds of plates, biscuit-formed with small holes and some with fewer, larger holes. In external appearance the two forms are quite different; *floridana* is variable in color, spotted or uniformly colored and is not thick-skinned. With the exception of very small specimens, *mexicana* is always uniform dark colored with paler ventral side. In a single specimen in the present collection large dark spots also are found on the ventral side. The skin in young specimens is thick and leathery. Their distribution is different. In some localities in Cuba and at a single point in Florida the areas of distribution overlap,

but elsewhere *mexicana* is found only in the eastern part of the West Indian waters, to Curacao, while *floridana* ranges from the Keys of Florida to Colon, Panama. *Mexicana* is undoubtedly identical with *H. africana* Theel from West Africa.

Falmouth Harbor, Antigua.

[*Holothuria mexicana* was common in Falmouth Harbor, in eel-grass, along with *Diadema* (*Centrochinus*), *Toxopneustes variegatus* and *Tripneustes esculentus*. In the shallow water which became quite warm at noon, were quantities of *Manicina* corals, and *Millepora alcicornis* of the most branched form. The animals rest motionless upon a bottom of very fine sand or mud, often slimy with organic matter, and the fine particles adhere to the skin of the holothurians. In aquaria at night the animals were more active than in the same situation during day.

The color is some shade of brown, often nearly black, with pale yellowish, pale brownish or pink ventral surface. Rarely the ventral side has large dark brown spots.—W. K. F.]

Holothuria glaberrima Selenka

Holothuria glaberrima Selenka, 1867, p. 328, pl. XVIII, fig. 57-58.—Semper, 1868, p. 92.—Lampert, 1885, p. 65; 1896, p. 56-59.—Theel, 1886, p. 33.—Clark, 1901, p. 259; 1919, p. 63.—Sluiter, 1910, p. 333.
Holothuria lubrica var. *glaberrima* Mitsukuri, 1912, p. 96.

This form seems to occur all over the West Indies; it is not found at Bermuda. It is known from Honduras and many localities on the north coast of South America. Without doubt Selenka is in error in recording it from the Gulf of Panama. Lampert has clearly pointed out the differences between this form and the nearly related *H. lubrica*, with which it has been confused. The color is uniformly brown with paler, more greyish ventral side; sometimes a single pale brown specimen occurs among numerous typical.

52 specimens from English Harbor, Antigua. 2 specimens from Bathsheba, Barbados.

[The habitat of this species is entirely different from that of any other holothurian encountered by the expedition. It is found only on rocky shores, exposed to the buffeting surges of the open sea, where it dwells in miniature basins of the rocks associated with *Echinometra lucunter*. These little hollows are the forms once occupied by *Echinometra*. When the tide is out, the hollows retain usually a little water, which is replenished with air-charged, foamy brine each time a breaker cascades back into the sea. I noticed that

the tentacles are kept expanded in such little pools. In hollows of sufficient size, several animals are wedged tightly together. They are difficult to dislodge, and it is easy to see how the unusual number of tube-feet aid the animal in clinging where the clawing waves are seldom at rest. There is usually a plentiful growth of short, tough kelp where the holothurians live. This kelp overhangs the edges of the little basins in which two or three of the animals are domiciled in such a way as practically to hide them.

The species is easily recognized by its very dark brown color, large, practically dendritic, tentacles and very crowded ventral pedicels.—W. K. F.]

Holothuria fossor n. sp.

Stichopus rigidus Selenka, (partly), 1867, p. 317, pl. XVIII, fig. 30-31.

Holothuria rigida Semper, 1868, p. 79.—Theel, 1886, p. 231.

Holothuria pleuripus Sluiter, 1910, p. 333.

Holothuria hypamma ♀ Clark, 1921, p. 178.

Holothuria hypamma Clark, 1922, p. 231.

Length 85 mm. Ventral side flattened, dorsal somewhat arched; skin very stiff and rigid, but thin; mouth ventral, the crown of very small and pale tentacles surrounded by a collar of papillæ; anus terminal.

Color, on dorsal side greyish, with about 12 pairs of indistinct spots; ventral surface white, rusty on the middle; and also a ring of rusty red pigment is found around the end of the pedicels. The appendages are small and inconspicuous. On the dorsal side, small wart-like papillæ of different sizes; they are numerous along the edge; ventrally, small retracted pedicels are found, not crowded; they are mostly retracted in the odd ambulacrum, laterally they are more conspicuous on account of the pigmentation.

A small and delicate calcareous ring is present; the posterior edge is undulated; the radialia are broad, squared, with a deep anterior notch; the interr radialia are small, with the usual anterior tooth. Tentacle ampullæ small and slender. The vascular ring is about 10 mm. distant from the calcareous ring; one slender Polian vesicle is present and a small stone canal, with small head, free on the right, partly attached to the mesentery. The genital tuft contains numerous long and dichotomously branched tubes, some of which, in the present specimen, are longer than the animal. Two respiratory trees, as usual the left is entangled in the well-developed

rete mirabile. The muscle bands are broad and thick; the circular musculature, very feeble. Plate II.

According to Selenka the Cuvierian organs are branched. There was found a brown mass near the base of the right respiratory tree, but it was impossible to trace any structure in it.

Deposits: In the body wall is found a layer of densely placed large tables, underneath a thick layer of strongly knobbed buttons.

The tables have a knobbed margin, the disk (.059 mm. diam.) has a large central hole and several marginal, but often the primary disk is covered by a secondary network, which hides the original structure; the spire has numerous blunt teeth, which unite and form a network. From the edge of the disk arise rods which unite with projections from the spire. The tables are larger and more complicated dorsally; ventrally they are smaller (.044 mm.) and represent different stages of development. The buttons are smallest and most knobbed dorsally, where they have six holes and are about half as long as the diameter of the tables (.039 mm.); ventrally they have ten to twelve holes and they are twice as long and often nearly flat (.0604 mm.).

In the dorsal papillæ are numerous curved supporting rods (.0832 mm.) but no end plate; in the pedicels the supporting rods (.0858 mm.) are nearly straight; they are broad, with few holes in the ends and on the middle; often they have a low longitudinal ridge; a small end plate is present.

In the pedicels the tables are especially small and of very variable development; Selenka most probably described these simple tables as those with eight rods in the spire. His spinous ellipses are without doubt, the dorsal tables, seen in oblique position.

Clark first noted that the *rigida* from Florida was different from the species of the Society Islands, which is regarded as the type (1921, p. 178). He regards the West Indian species as identical with his *H. hypamma* from Murray Islands (1922). The undeveloped tables in the pedicels of the West Indian species resemble the average tables of *H. hypamma* (.054 mm.); but those found in the body wall of *H. fossor* are large and much more complicated. The buttons are entirely different; they are much more knobbed in the West Indian species, the holes are smaller and they never have the middle bar projecting over the ends of the buttons, as in *H. hypamma*.

Sluiter has recorded a specimen of *H. pleuripus* (Haacke) from Kingston, which he states agrees with the description given by Theel

of some specimens, in the Godeffroy Collection, from Fiji and Tahiti. Undoubtedly Sluiter is dealing with an example of *H. fossor*, which may be inferred from Theel's description of *H. pleuripus*, more easily than from Selenka's description of *H. rigida*. It has been possible to make sure of the identification by comparing spicules of *H. fossor* with those of Selenka's type of *H. rigida* in the Museum of Comparative Zoology.

Inasmuch as the species from the Society Islands is the genuine *Holothuria rigida* (Selenka) and that from the West Indies is different from Clark's *H. hypamma* (Murray Islands), it becomes necessary to name the West Indian form. Dr. Fisher has proposed the name *H. fossor*, on account of its burrowing habit.

1 specimen, Falmouth Harbor, Antigua.

[This species has less "behavior" than a sluggish chiton. It was found under rocks, which rested on sand, Falmouth Harbor, and was never uncovered by tide. It was deeply buried, after the manner of *Brissus brissus*, and probably does not come to the surface, unless at night. In the aquarium it was very sluggish both by night and by day. In life it is covered with fine sand grains.—W. K. F.]

ACTINOPYGA

Anal teeth very small, dorsally warts, ventrally pedicels.

Color uniform brown, with a greenish shade, (the green pigment is extracted in alcohol). Deposits: Tables with numerous holes in the brim and medium sized spire ending in numerous teeth, buttons with 6 holes, elliptical and often curved and irregular. Cuvierian organs present. 20 tentacles. Small form (4.5 cm.). *Actinopyga parvula* (Selenka).

Actinopyga parvula (Selenka)

Mulleria parvula Selenka, 1867, p. 314, pl. XVIII, fig. 17-18.—Semper, 1868, p. 77.—Lampert, 1885, p. 76.—Theel, 1886, p. 199.—Sluiter, 1910, p. 333. *Holothuria captiva* Ludwig, 1874, p. 32.—Lampert, 1885, p. 68.—Theel, 1886, p. 220.—Verrill, 1907, p. 321.—Crozier, 1917, p. 560.—Clark, 1919, p. 63, 64. *Actinopyga parvula* Clark, 1919, p. 63.—Deichmann, 1921, p. 199-215, text fig. 1-3, 5-7.

As usual this form is abundant. All kinds of animals are present, from complete, normal ones to small balls of skin, lacking either oral or anal end, representing regenerating stages. The anal teeth are very small and usually this species has been recorded as *H. captiva* Ludwig. Even when the anal teeth are not found, in regenerating stages, this species is easily recognized by its comparatively small size, its uniform brown color, and the peculiar green pig-

ment which the body-wall contains. None of the West Indian holothurians with dorsal warts and ventral crowded pedicels, has spicules developed as tables and buttons. The type was described from Florida. It is known from the West Indies to Bermuda.

93 specimens from English Harbor, Antigua. 5 from Barbados.

[This species, the *Holothuria captiva* of the "Narrative," was abundant under stones at Harbor Point, English Harbor, in the same locality as *H. surinamensis*, and was found sparingly under stones at Falmouth Harbor. It is very warty, rich bright brown, with yellow tentacles and not over two and a half inches long. It shoots out its delicate viscid Cuvierian organs with great freedom and precision. A small spider crab which was bombarded with the Cuvierian filaments was visibly embarrassed as the threads stretched out at each movement of his legs. He solved the difficulty by eating the threads.—W. K. F.]

STICHOPUS

Deposits: Tables and small C-shaped bodies, 1-2 times as large as the height of the tables. Strongly developed warts on back and side. Color very variable, often greyish brown with darker spots or patches.

Stichopus badionotus Selenka.

Deposits: Tables and C-shaped bodies, 3-4 times as large as height of tables; only small warts on back and side. Color yellow with brown, dotted irregularly; tip of papillae pale. *Stichopus macroparentheses* Clark.

Stichopus badionotus Selenka

Stichopus badionotus Selenka, 1867, p. 316, pl. 18, fig. 26.—Clark, 1922, p. 55, pl. 2, fig. 11-15, (complete list of references).

The specimens show the usual variation in color and pattern. This species ranges from the Atlantic coast of Panama to Bermuda; according to Clark, 1919, it does not occur south of Antigua. Clark has compared specimens from the West Indies with *Stichopus* from the West Coast of Mexico and believes that the two species are identical. He also places Greef's *Stichopus maculatus*, from Rolas, West Africa, as a probable synonym of *badionotus*.

8 specimens, English Harbor, Antigua.

[This conspicuous species was abundant in English and Falmouth Harbors among eel-grass, on a soft, sandy bottom.—W. K. F.]

Stichopus macroparentheses Clark

Stichopus macroparentheses Clark, 1922, p. 61, pl. I, fig. 1-7.

The two specimens are larger than those which Clark found at Jamaica and Birds Key. Both specimens agree with the description

of the type, in the shape of the calcareous ring and the deposits. They are not very well suited to complete description as one specimen is flattened and formless and the other blown up to a thin-walled sac. It is apparent that the pedicels are in three rows and the warts are small and inconspicuous. The genital organs are totally absent in the first specimen and small in the other. The color is yellow or pale brown with darker brown spots, and the ends of the papillæ are pale. They are said in a younger stage to resemble young *S. badionotus*.

2 specimens from English Harbor, on sand among eel-grass.

MESOTHURIA

Skin semitransparent. Deposits: Tables alone, with large central hole, surrounded by smaller; spire high and slender with up to 3-4 cross beams ending in four blunt teeth. Few pedicels, dorsally papillæ. Small form (1.2 cm.). *Mesothuria verrilli* Theel.

Mesothuria verrilli (Theel)

Holothuria verrilli Theel, 1886 b, p. 6.—Marenzeller, 1893, p. 79, pl. I, fig. 2, pl. II, fig. 2.

Holothuria intestinalis Koehler, 1895, p. 482; 1896, p. 106.—Ludwig, 1900, p. 138.

Holothuria intestinalis var. *verrilli* Herouard, 1896, p. 163.

Holothuria magellani ? Sluiter, 1910, p. 332.

Mesothuria verrilli Oestergren, 1896, p. 347.—Perrier, 1902, p. 357, pl. XVI, fig. 22-31.

The single specimen (Plate I, fig. 2,) is less than 10 mm. long, whitish gray and rough from the numerous deposits. The dorsal appendages are scattered and without end-plate; ventrally they are indistinctly placed in three more or less double rows, and the end plate is well developed. The tables have a central large hole and a different number of marginal holes; the spire is very variable in height and upward of four cross beams have been found. It usually ends in four teeth.

Sluiter has found a specimen from nearly the same locality which he refers to *M. magellani* (Ludwig) and says it is very near to the European *M. intestinalis* (Asc. and Ratke). If the character "no pedicels in the midventral radialia" is constant, the present specimen can not be *magellani*. It may possibly be *M. verrilli* Theel, which has been recorded from Barbados, but in a depth of 399 fathoms. The only difference is that Theel speaks of pedicels all over the body. He also describes the tables with one to two cross

beams, but mentions that there is a very wide range of variation in the tables. He does not figure the spicules. The present specimen seems just as likely to be referable to *verrilli*, normally occurring at a great depth as it is to *magellani*, from the Straits of Magellan.

Both forms are nearly related to *M. intestinalis* to which Koehler and Ludwig unite them; Oestergren, however, has compared *M. verrilli* with numerous specimens of the European *intestinalis*, and says that they are different.

1 specimen from Falmouth Harbor, Antigua.

KEY TO THE SPECIES OF THYONE

- a¹ Calcareous ring simple; small anal teeth present; tentacles of equal size; end-plate and supporting rods present in the pedicels. Deposits: Four-holed buttons and four-spoked cups with 8-12 teeth in the margin. Perforated plates and rods numerous near the anal end. Color greyish-brown, mottled with darker brown.
 - b¹ Numerous strongly knobbed buttons with small holes, some few with knobs on the margin and larger holes. Skin stiff with spicules.
Thyone surinamensis Semper.
 - b² Few buttons with large holes and knobs on the margin. Skin soft, with few spicules. *Thyone suspecta* Ludwig.
- a² Calcareous ring with short posterior prolongations; no anal teeth; tentacles of unequal size, the two ventral being smaller. Deposits: Tables with reduced spire and few rosettes. Well developed end-plate but no supporting rods in the numerous soft pedicels.
 - b¹ Deposits: Tables with spire reduced to 2 knobs and 4 holes in the oval disk. No separate posterior pieces on the interraddialia of the calcareous ring. Color violet. *Thyone trita* Sluiter.
 - b² Deposits: Tables with spire reduced and regular disk with 8 holes and 8 marginal teeth. Separate posterior pieces on the interraddialia, sometimes forming short tails. Color uniform brown.

Thyone constituta Sluiter.

Thyone suspecta Ludwig

Thyone suspecta Ludwig, 1874, p. 16, pl. 6, fig. 19.—Lampert, 1885, p. 157.—

Theel, 1886 a, p. 133.—Sluiter, 1910, p. 333.—Clark, 1919, p. 63.

Thyone braziliensis Verrill, 1868, p. 370.—Rathbun, 1879, p. 141.

The single specimen (Plate III, fig. 2,) is from the same locality as the type. It agrees in every respect with the description of the type and with some specimens from Savanilla, Colombia, except that the end-plate is either small or composed of a central larger part and several smaller peripheral pieces. Many of the cups are poorly developed. This might seem to be caused by the formalin in which the specimen has been preserved, but in the anal region

as well as in the extended introvert the cups are very well developed.

The skin is thick and soft and the pedicels are uniformly spread over the entire body. The anal teeth are present but not very prominent. The spicules are most numerous in the anal part, where large perforated plates are accumulated in addition to the ordinary buttons which have large holes and small isolated knobs on the rim. All stages are found from complete bodies to dichotomously branched ones with the ends of the branches united. The layer of buttons is very scattered.

The cups are not numerous, they are four-spoked with 12 spines on the edge. In the pedicels are simple supporting rods, nearly straight, with large holes and narrowest on the middle. In the introvert, besides numerous cups, are found heaps of rosettes. The rods in the tentacles are of the same type as the supporting rods in the feet, but they are more irregular and branched.

The internal anatomy is normal for the genus; the calcareous ring is simple, deeply incised posteriorly, and anteriorly with large teeth of nearly equal size. One Polian vesicle is present; one dorsally embedded stone canal; the muscular stomach is short; the long and unbranched tubes of the genital organs are filled with eggs and fastened near the middle of the body wall, where the retractors arise; the longitudinal musculature is well developed.

Distribution: Colombia to Barbados; not common.

1 specimen from Barbados.

Thyone trita Sluiter

Thyone trita Sluiter, 1910.

This species has only been recorded from Barbados and only the type specimens are existing. The two present specimens agree well with Sluiter's description. The smallest is very dark, with a shade of violet.

2 specimens from English Harbor, Antigua.

Thyone constituta Sluiter

Thyone constituta Sluiter, 1910.

The single specimen is better developed than the type, which was found at Barbados. The calcareous ring has the same narrow long radialia with short posterior prolongations and the interradialia are broad and overlap the middle of the radialia; but the separate posterior pieces form real short prolongations. As in *T. trita* the pedicels are numerous, small, and soft, with well developed end

plate. The very characteristic tables are, near the oral end, more irregular, with numerous teeth and holes, instead of the ordinary eight teeth and eight holes. The rosette shaped bodies are most numerous in the introvert and more scattered in other parts of the body wall, but they are not very common.

1 specimen from English Harbor, Antigua.

Thyone surinamensis Semper

Thyone surinamensis Semper, 1868, p. 65, pl. XV, fig. 15.—Lampert, 1885, p. 158.—Theel, 1886, p. 133.

Cucumaria punctata Ludwig, 1874, p. 82.—Sluiter, 1910, p. 335.—Clark, 1919, p. 63.

Semperia punctata Lampert, 1885, p. 152.

The specimens (Plate III, fig. 1,) except in minor details agree with the description given by Semper. The genital organs are unbranched, but so numerous and twisted around each other, that they appear to be divided. The pedicels are, in some specimens, not uniformly distributed, but absent from a narrow strip on each interradial area. These animals could therefore be referred to *Cucumaria punctata* (Ludwig), which was described from Barbados. The only anatomical difference is that the type of *C. punctata* had 5 Polian vesicles, while the present animals have only one or two. The deposits are of the same type—four-holed knobbed buttons, and cups. A preparation of spicules of a *C. punctata* from Bermuda shows that the cups have, besides about 12 marginal teeth, a variable number of teeth projecting outward. The same is the case of the cups from the present animals. The spicules from the animals with uniformly distributed pedicels can not be separated from those with naked strips on the interradialia; it seems therefore very probable that Ludwig's *C. punctata* is a younger stage of *Thyone surinamensis*.

In coloration and size the present species is similar to *T. suspecta* and the internal anatomy is almost identical. In *T. surinamensis* there are two kinds of buttons: strongly knobbed, with small holes, present in large number, and some few with larger holes and isolated knobs on the margin. These are perhaps stages of the strongly knobbed buttons. In *suspecta* there is only one kind of button, with large holes and isolated knobs; usually they are larger than the average button in *surinamensis*. The cups, supporting rods and rosettes are of exactly the same type. It might be inferred from a mere description, that the two species are the same and that

suspecta is only a form in which the large layer of strongly knobbed buttons has not been developed. The figures of the spicules show the actual differences, which are found in the two species. Most of the buttons are smaller in *surinamensis*; the cups are larger in absolute size and in proportion to the buttons. They seem to have more accessory teeth in *surinamensis*, but that may be accidental. The supporting rods are slightly longer in *surinamensis* and often have a nearly straight edge. The holes are small, while *suspecta* has very large holes in the supporting rods and a very undulated margin. The rosettes are much larger in *surinamensis* than in *suspecta*.

Distribution: From northern coast of South America to Barbados (and if identical with *Cucumaria punctata* also from Bermuda.) Pelican Island, Barbados.

Phyllophorus parvum (Ludwig)

Thyonidium parvum Ludwig, 1881, p. 54-55, pl. III, fig. 16-18.—Lampert, 1885, p. 169.

Eighteen to twenty tentacles in two circles and of different length; skin leathery; the pedicels are not crowded and only indistinctly placed in rows. Deposits: Tables with large rounded or squared disk with two small central holes and 8-10 larger in the margin; spire built up of two rods and ending in few teeth; no supporting rods; small end-plate. Calcareous ring with long posterior prolongations. Color pale reddish brown with violet tentacles.

The single specimen agrees with Ludwig's description. The tentacles are deep violet and of varying size. According to Lampert, this species is common along the coast of Brazil down to Rio Janeiro. It seems never to have been taken in the West Indies.

One specimen from English Harbor, Antigua.

Euapta lappa (J. Müller)

Synapta lappa J. Müller, 1850, p. 134.

Euapta lappa Clark, 1907, p. 73, pl. IV, fig. 23-25. (Complete literature list). 1924, p. 464, pl. I, fig. 5-7.

The present specimens are all large and typical in color and spicules. This species which is the largest apodous form in the West Indies, is, according to Clark, known from Florida to Tobago and also from Teneriffe (Theel).

2 specimens from Falmouth Harbor; 2 from entrance of English Harbor, Antigua.

[This large, showy, and active synaptid was found among stones

at English Harbor (Harbor Point), and at Falmouth Harbor. Professor Nutting, in the narrative of the Barbados-Antigua Expedition, p. 194, writes of it as follows:

"A fully extended specimen sometimes reaches the length of two feet and looks more like an enormous worm than like anything else. It is quite translucent, being thinner walled than most species, and the body is longitudinally striped with reddish brown bands and bears numerous rounded nodules arranged in annular series; but these disappear completely when the animal is entirely extended, or in parts of its length which are extended, only to reappear instantly upon contraction. Waves of such contraction pass rhythmically along its length. It is the most active holothurian by far that I have ever seen and is really a beautiful object when in the aquaria and in vigorous motion. The feathery tentacles are in constant activity, waving this way and that, lengthening and shortening, bending gracefully, their frilled edges a constant play of activity; while the whole body is in rhythmical movement, bending, twisting, elongating, retracting, and at the same time pulsating with the waves of retraction already referred to, during which the hemispherical nodules appear and disappear as if by magic along its whole length. The transparency of the body walls gives a peculiar delicacy that we do not usually associate with the ordinary unattractive 'sea cucumbers'.

"Its footless condition is compensated for by the possession of several peculiar features. Doubtless the hemispherical and temporary nodules already referred to give it a hold on the stones between which it worms its way, and its extreme distensibility enables it to go through quite narrow holes and cracks, while the waves of contraction serve to push it rapidly along either the surface of the sand bottom or over and between rocks. It can also swim to a limited extent and will frequently raise itself on end in the aquaria so as to assume a vertical position with the tentacles exploring the surface while the aboral end rests on the bottom."—W.K.F.]

Synaptula hydriformis (Lesueur)

Holothuria hydriformis Lesueur, 1824, p. 162.

Synaptula hydriformis Clark, 1907, p. 82, pl. VI. (Complete literature). 1924, p. 473, pl. III, fig. 5, pl. IV, fig. 4.

A single small specimen about 20 mm. long, nearly colorless, with typical spicules. This form is common from Brazil to Florida and is also found at Bermuda (Clark).

One specimen from Antigua.

Chiridota rotifera Pourtales

Chiridota rotifera Pourtales, 1851.—Clark, 1907, p. 115, (complete list of references); 1919 p. 63.—Sluiter, 1910, p. 341.

This species seems not to have been taken at Antigua before, but it is a common form which according to Clark has the same distribution as *S. hydriformis*.

2 specimens from Antigua.

BIBLIOGRAPHY

Brandt J. F.

- 1835 Prodrömus descriptionis animalium ab H. Mertensio in orbis terrarum circum navigatione observatorum. Fasc. I, pp. 42-61, Petropoli.

Clark H. L.

- 1898 Notes on the Echinoderms of Bermuda. Ann. N. Y. Acad. Sci., Vol. XI, pp. 407-413, New York.
- 1899 Further Notes on the Echinoderms of Bermuda. Ann. N. Y. Acad. Sci., Vol. XII, pp. 117-138, pl. IV, New York.
- 1901a Bermudan Echinoderms etc. Proc. Bost. Soc., Vol. XXIX, pp. 339-345.
- 1901b The Echinoderms of Porto Rico. Bull. U. S. Fish Comm., Vol. XX, pt. II, pp. 231-263, pls. XIV-XVII, Washington.
- 1901c Synopsis of North American Invertebrates. XV, The Holothurioidea. Amer. Nat. XXXV, pp. 479-495, 27 text fig.
- 1907 The Apodous Holothurians. Smithsonian Contr. Vol. XXXV, pp. 231, pls. I-XIII. Washington.
- 1919 Distribution of the Littoral Echinoderms of the West Indies. Dept. Mar. Biol. Carnegie Inst. Vol. XIII, pp. 47-74. Washington.
- 1921 The Echinoderm Fauna of Torres Strait, etc. Dept. Mar. Biol. Carnegie Inst. No. 10, pp. 224, pls. I-XXXVIII. Washington.
- 1922 The Holothurians of the Genus *Stichopus*. Bull. Mus. Comp. Zool. Vol. LXV, No. 3, pp. 39-74, pls. 1-2. Cambridge, Mass.
- 1924 The Holothurians of the Museum of Comparative Zoology: The Synaptinae. Bull. Mus. Comp. Zool. Vol. XV, No. 13, pp. 459-501, pls. 1-12. Cambridge, Mass.

Crozier W. I.

- 1914 The sensory reactions in *H. surinamensis*. Zool. Jahrb. Abt. Allg. Zool. Physiol. Vol. XXXV, No. 3, pp. 577-584. Reprinted in: Contr. Lab. Mus. Comp. Zool. Harvard Coll. No. 251, 1915.
- 1916 The rhythmic pulsation of the cloaca of Holothuria. Jour. Exp. Zool. 20, pp. 297-356. Philadelphia.
- 1917 Multiplication by fission in Holothuria. Amer. Nat. 51, pp. 560-566. New York.

Deichmann E.

- 1921 On some cases of multiplication by fission etc. Papers from Dr. Th. Mortensen's Pacific Exp. 1914-16, Vid. Med. Nat. For. Bd. 73, pp. 199-215. Copenhagen.

Edwards Ch. L.

- 1905 A quantitative study of *H. atra* Jaeger and the re-establishment of *H. floridana* Pourt. (*H. mexicana* Ludwig). Science N. S. Vol. XXI, pp. 383-384.
- 1908 Variation, Development and Growth in *H. floridana* Pourt., Biometrika, pp. 254-301, pls. I-V.

- Fisher W. K.
1907 The Holothurians of the Hawaiian Islands, Proc. U. S. Nat. Mus. Vol. XXXII, pp. 637-744, pls. LXVI-LXXXII.
- Forskaal P.
1775 Descriptiones animalium quae in itinere orientali observavit P. Forskaal; post mortem auctoris editit C. Niebuhr, pp. 121-122. Havniae.
- Greef B.
1882 Echinodermen, beobachtet auf eine Reise nach der Guinea Insel Sao Tome, Zool. Anzeiger, 5, p. 158.
- Heilprin A.
1888 Contribution to the Natural History of the Bermuda Islands. Proc. Acad. Nat. Sci. Phila. Pt. 40, pp. 302-328.
- Herouard E.
1896 Note preliminaire sur les Holothuries provenant des dragages du yacht "Princesse Alice". Bull. de la Soc. Zool. de France, T. XXI, pp. 163-168.
- Koehler R.
1895 Dragages profondes executés a bord du "Caudan" dans le golfe du Gascogne Aout—Septembre 1895. Rapport preliminaire sur les échinodermes, Rev. Biol. du Nord de la France. Vol. VII, pp. 478-496.
1896 Résultats scientifique de la campagne du "Caudan" dans le golfe de Gascogne Aout—Septembre 1895. Ann. de l'Université de Lyon, Fasc. I, Vol. XXVI, pp. 33-127, pls. I-IV.
- Lampert K.
1885 Die Seewalzen, Reisen im Archipel der Philippinen von Dr. C. Semper, Theil II, Bd. IV, Abt. III, pp. 310, pl. 1. Wiesbaden.
1896 Die von Dr. Stuhlmann in den Jahren 1888 und 1889 an der Oestkust Afrikas gesammelten Holothurien. Mitt. Mus. Hamburg, Bd. XIII, pp. 49-71. Hamburg.
- Lesueur C. A.
1823 Description of several new species of Holothurioidea, Jour. Acad. Nat. Sci. Phila. Vol. IV, pp. 155-163.
- Ludwig H.
1874 Beitrage zur Kenntniss der Holothurien. Arb. Zool. Zoot. Inst. Bd. II, Heft 2, pp. 77-118, pls. VI, VII. Wurzburg.
1881a Revision der Mertens-Brandt'schen Holothurien. Zeit. Wiss. Zool. Vol. XXXV, pp. 575-599.
1881b Ueber eine lebendige gebaerende Synaptide und zwei andere neue Holothurien-arten der Brazilianischer Kuste. Arch. Biol. T. II, pp. 41-58, pl. III. Liege.
1883 Verzeichniss der Holothurien des Kieler Mus. Bericht. Oberh. Gesell. Nat. Heilk. Bd. XXII, pp. 155-176. Giessen.
1900 Arktische und Subarktische Holothurien. Fauna Arctica. Bd. I, Lief. 1, pp. 135-178. Jena.
- Marenzeller E. V.
1893 Contribution a l'étude des Holothuries de l'Atlantique du Nord

- (Golfe de Gascogne, Isles Açores). Résul. Comp. Sci. Prince de Monaco, Fasc. VI, pp. 1-22, pls. 1-2. Monaco.
- Mitsukuri
1912 Actinopodous Holothurians. Jour. Coll. Sci. Tokyo, Vol. XXIX, Art. 2, pp. 284, pls. I-VIII.
- Müller J.
1850 Anatomische Studien ueber die Echinodermen. Müllers Arch. pp. 129-147, 225-233.
1854 Ueber den Bau der Echinodermen. Abh. Berl. Akad. Wiss. aus d. Jahre 1853, pp. 96, pls. 9. Berlin.
- Oestergren H.
1896 Zur Kenntniss der Subfamilie der Synallactinæ. Festschrift W. Lilljeborg, pp. 345-369, pl. XVIII. Upsala.
- Perrier R.
1903 Holothuries. Exped. du Travailleux et Talisman, pp. 273-552, pls. I-XI. Paris.
- Pourtales L. F.
1851 On the Holothuridæ of the Atlantic Coast of the United States. Proc. Amer. Ass. Adv. Sci. Fifth Meeting, pp. 8-16, Washington.
- Rathbun R.
1879 List of the Brazilian Echinoderms, etc. Trans. Connect. Acad. Vol. XV, pt. 1, pp. 139-158.
- Selenka E.
1867 Beiträge zur Anatomie u. Systematik d. Holothurien, Zeit. Wiss. Zool. Bd. XVII, pp. 291-374, pls. XVII-XX. Leipzig.
- Semper C.
1868 Reisen im Archipel der Philippinen. Theil II. Wiss. Res. Bd. 1, Holothurien, pp. 228, pls. I-XL. Leipzig.
- Sluiter C. Ph.
1910 Westindische Holothurien, Erg. Zool. Forschungsreise nach Westindien von W. Kukenthal u. R. Hartmeyer. Zool. Jahrb. f. Anat. u. Syst., Suppl. XI, Heft 2, pp. 331-341. Jena.
- Stimpson W.
1860 Zoological Notices on the Genus *Synapta* by Woodward and Barrett. Amer. Jour. Sci. Vol. XXIX, p. 134. New Haven.
- Theel H.
1886a Report on the Holothurioidea. Pt. II. Rep. Sci. Res. H.M.S. "Challenger," Zool. Vol. XIV, Pt. 39, pp. 290, pls. I-XVI. London.
1886b Report on the Holothurioidea. Bull. Mus. Comp. Zool. Vol. XIII, pp. 1-21, pl. 1. Cambridge, Mass.
- Verrill A.
1868 Notice of the corals and echinoderms collected by Prof. C. F. Hartt at the Abrolhos Reefs, Province of Bahia, Brazil, 1867. Trans. Conn. Acad. Vol. I, pp. 351-376. New Haven.
1901 Additions to the Fauna of Bermuda. Trans. Connect. Acad. Sci., Vol. XI, pp. 583-587.
1904-07 The Bermuda Islands. Geology. pp. 144-145, 320-322. Text fig. 37-39, 171-173, Trans. Connect. Acad. Sci. Vol. XII.

EXPLANATION OF PLATES

PLATE I

Holothuria surinamensis Ludwig, x670

- 1a Disk of table from very young specimen
- 1b Lateral view of table from very young specimen
- 1c Top of spire seen from above, of old specimen
- 1d-e Tables with completely absorbed disk, lateral view
- 1f Half of rod from skin of old specimen
- 1g Rod from near the end of pedicel of old animal

Mesothuria verrilli Theel

- 2a Lateral view of table
- 2b Disk of table from above

PLATE II

Holothuria fossor n.sp., x670

- 1a-b Supporting rods from pedicel
- 1c Flattened button from ventral side
- 1d Knobbed button from ventral side
- 1e Small, relatively simple table from pedicel
- 1f Disk of very simple small table from pedicel
- 1g-h Buttons from dorsal side
- 1i-j Supporting rods from papilla

PLATE III

Thyone surinamensis Semper, x670 (except 1c and 2a)

- 1a Knobbed button
- 1b-c Baskets, seen from above
- 1d Baskets, lateral view
- 1e Supporting rods from pedicel, x270

Thyone suspecta Ludwig

- 2a Supporting rods from pedicel, x270
- 2b-c Baskets, lateral view
- 2d-e Buttons

PLATE I

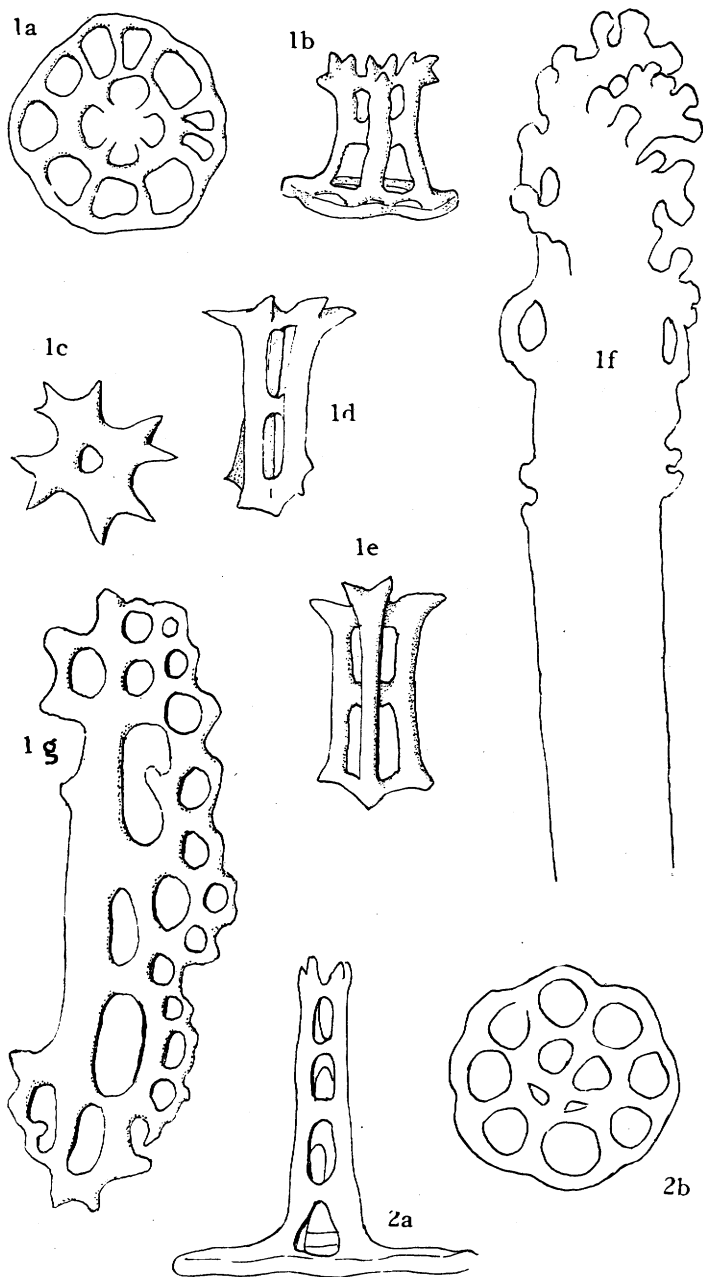


PLATE II

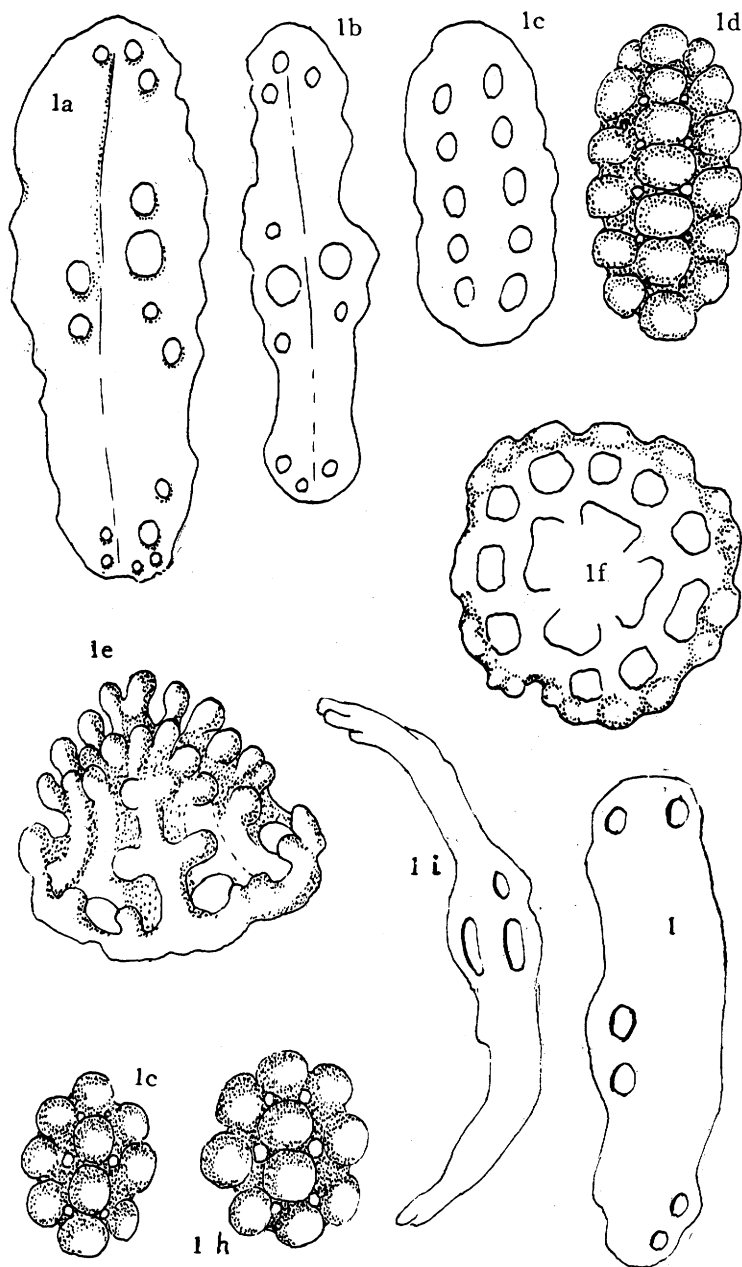
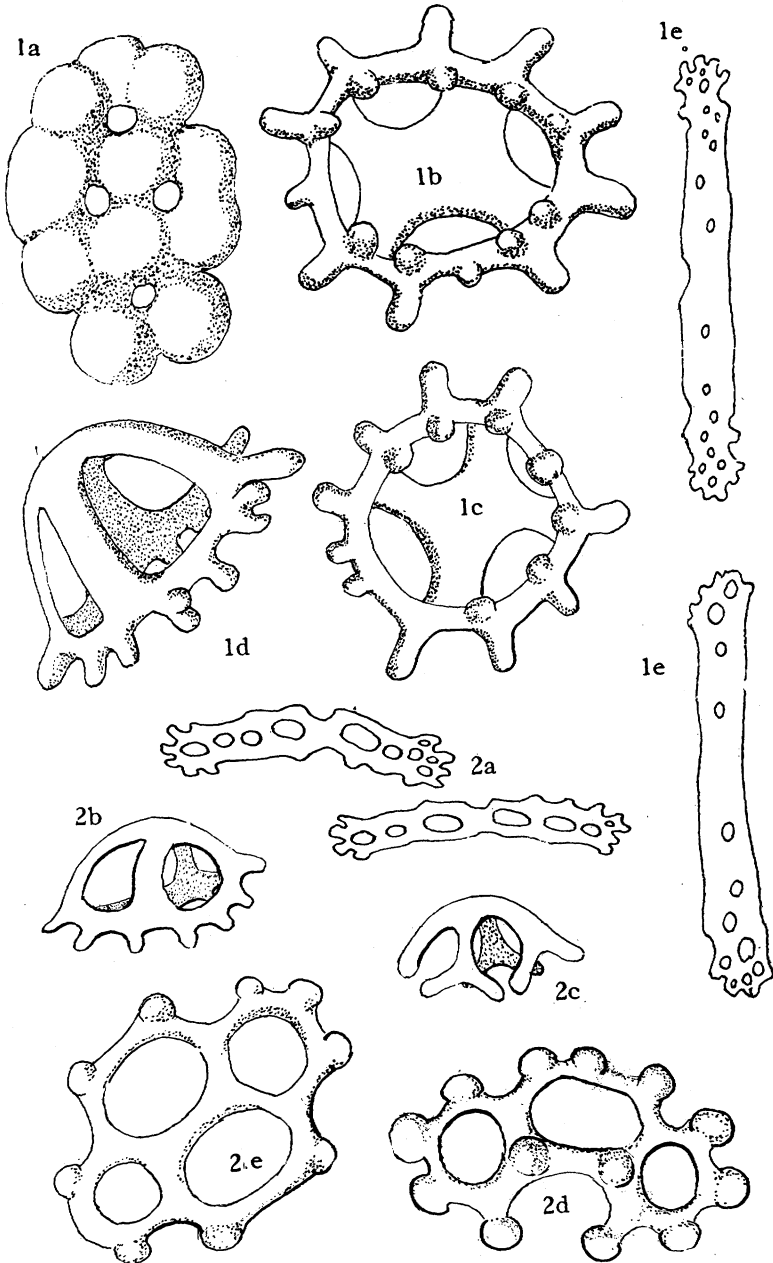
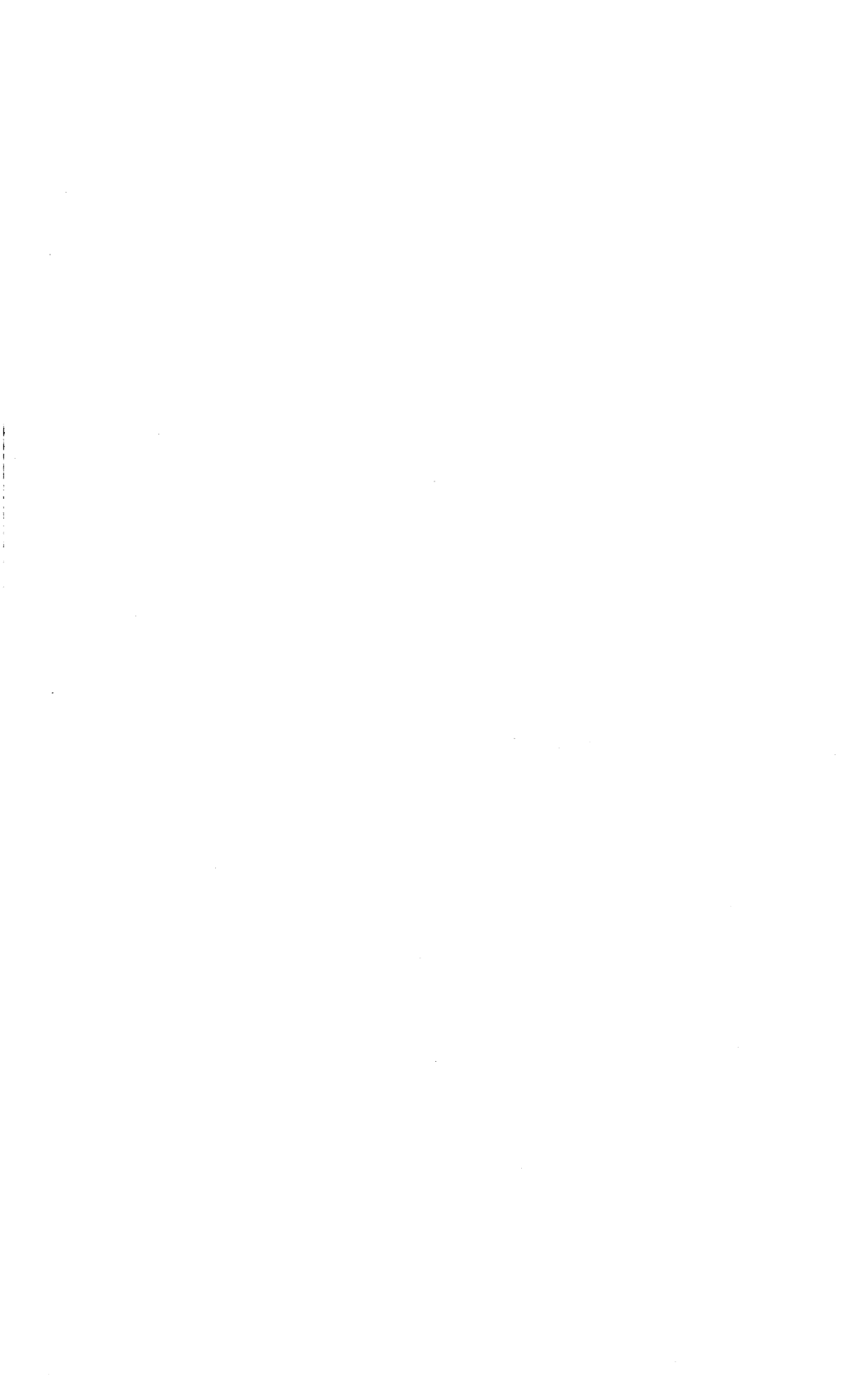


PLATE III





LEPIDOPTERA

Collected by the Barbados-Antigua Expedition from the
University of Iowa

A. W. LINDSEY
Denison University

The delicacy of Lepidoptera necessitates special care in the collecting and handling of these insects which is not at all compatible with extensive work on other orders. It is therefore not surprising that Dr. Stoner's catch of butterflies and moths, submitted to me, is small, nor that it is made up mostly of species common in the islands. More surprising, indeed, is the fact that this small lot includes two undescribed species, a Syntomid moth, which I am pleased to name in the following pages in honor of Dr. Stoner, and a Cossid.

The specimens included in the lot are listed below. With few exceptions the species represented occur also in the southern part of our own continent, while some are found even farther north.

Pieridæ

Pieris vlei Bdv. Antigua, June 24, 1 ♂, 5 ♀; July 1, 4 ♂, 2 ♀.

Catopsilia eubule Linn. Antigua, June 24, 1 ♀; July 1, 1 ♀; July 6, 6 ♂, 1 ♀.

Eurema euterpe Mén. Antigua, June 22, 1 ♂; 23, 1 ♂; 24, 1 ♂, 3 ♀; July 1 and 6, 6 ♂, 1 ♀. All females show a marked tendency to albinism.

Nymphalidæ

Heliconius charithonia Linn. Antigua, June 22, 1 ♂.

Dione vanillæ Linn. Bridgetown, Barbados, May 22, 1 ♂, 1 ♀; June 11, 1 ♂, 1 ♀. Barbados, May, 1 ♀; June 6, 1 ♂. Antigua, June 22, 2 ♂; June 24, 1 ♂.

Junonia genoveva Cram. Bridgetown, Barbados, May 16, 2 ♀; May 22, 2 ♀. Barbados, June 3, 1 ♂. Antigua, June 22 and 24, 1 ♂ each.

Phyciodes anocaona H.-S. Antigua, June 24, 1 ♀.

Lycænidæ

Lycæna hanno Stoll. Antigua, June 24, 1 ♂, 1 ♀.

Thecla acis Dru. Antigua, June 24, 1 ♀.

Hesperiidæ

Eudamus proteus Linn. Antigua, July 6 and 8, 1 ♀ each.

Brachycoryne arcas Dru. Antigua, June 22, 1 ♂.

Sphingidæ

Protoparce rustica Fab. Barbados, June, 1 ♂.

Xylophanes pluto Fab. Antigua, June 24, 1 ♂.

Syntomidæ

Horama stoneri n. sp.

Expanse of type 34 mm.

♀. Head black with a bright ochre spot between antennæ and two before eyes. Palpi also bright ochre. Antennæ black with ochreous tips. Collar with whitish ochreous spots at middle and sides, and an elongated spot, almost fulvous, below the latter. Patagia black with a bright ochre line near upper margin. Thorax black above with two bright ochre spots on mesonotum and two on metanotum, and a small pure white spot at humerus of each primary. Below with a white spot above coxa of each leg, the last four large but the first two small. Coxæ with a bright ochreous patch on each. Tibiæ and tarsi mostly ochreous. Tips of hind tibiæ and all of femora brownish. First abdominal segment strongly bullate on the sides. Anterior half of tergite of this segment silky white, separated by a brownish line from the bright ochreous posterior part. The ochreous portion extends almost completely over the bullæ. Remaining segments brown with slender terminal lines, ochreous on all but the first two where they are pure white ventrad and pale above.

The primaries approach cinnamon brown but are duller in shade. They are brightest at the base. Secondaries bright ochreous in the anal area, blending into buff at the costal margin and brown at the apex. The under surface of the primaries is almost evenly ochreous, of the secondaries a similar but brighter color.

Holotype ♀, Antigua, June 24. Two other females were taken June 21 and there is a male from the same island in the National Museum. This undoubtedly belongs to the same species, but since it is without an abdomen it is not being included in the type series.

Arctiidæ

Utetheisa ornatrix Linn. Barbados, May, 1 ♀; May 16-18, 20 specimens of both sexes; June 3, 2 ♂; June 8, 2 ♂, 1 ♀, and one broken specimen.

Noctuidæ

Melipotis contorta Gn. Antigua, June 28, 1 ♀.

Melipotis famelica Gn. Antigua, June 24, 3 ♀; July 1, 1 ♀.

Hyblæa puera Cram. Antigua, June 22, 1 ♂.

Aletia argillacea Hbn. Barbados, May 16, 1 ♂.

Cossidæ

Psychonoctua lillianæ, n. sp.

Expanse of type 48 mm.

♂. Vestiture of the body and head a mixture of chalky white and dull brown scales, giving the insect a hoary brownish-gray color.

The primaries are similar to the body, but with more brown scales grouped together in some parts. These form a brown basal patch with an oblique outer margin beginning about one third from base of wing on costa and running almost to base as it approaches the inner margin. In it there is a short longitudinal black dash just behind cell. In the type this has two short projections on the costal side and one between them on the opposite side. About one third from apex on costa a brown shade arises which runs to inner margin parallel with the outer limit of the basal shade. This contains a blackish crescent at end of cell. The median pale area thus enclosed is whiter than the rest of the wing. Terminal area slightly clouded with brown. Entire wing marked with transverse brown strigæ. Fringes whitish with brown tufts at ends of veins.

The secondaries are more evenly colored. They are brownish white with a few dark strigæ in the outer margin toward the anal angle. Fringes as in primaries.

On the outer surface the primaries are clouded with gray-brown, paler behind cell, slightly paler and strigate in terminal third, and faintly barred with white in basal two-thirds of the extreme costal area. Secondaries as above.

Holotype ♂, Antigua, July 1, collected by Mrs. Stoner for whom the species is named. I am indebted to Dr. Schaus for comparing the type with the material in the National Museum.

Through the kindness of Dr. Stoner the types of *H. stoneri* and *P. lillianæ* have been placed in the U. S. National Museum.

UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

VOLUME XI

NUMBER 8

PAPERS ON GEOLOGY

PUBLISHED BY THE UNIVERSITY, IOWA CITY, IOWA

CONTENTS

- Additional Cystoids and Crinoids from the Maquoketa
Shale of Iowa* A. O. THOMAS and H. S. LADD
- A Theory of Origin of Some Limestone Masses and
Septaria* A. L. LUGN
- Methods of Collecting Sediment Samples from the
Mississippi River* A. L. LUGN

ADDITIONAL CYSTOIDS AND CRINOIDS FROM THE MAQUOKETA SHALE OF IOWA

A. O. THOMAS and H. S. LADD

(PLATES I-VI)

An excellent paper has recently appeared on the echinoderms of the Maquoketa of Iowa.¹ It was based on collections made several years ago and found almost wholly within Fayette county. During the past two or three years the junior author has made an extensive study of the entire Maquoketa terrane in Iowa and in the course of that investigation has made large collections of fossils at many horizons and localities. The echinodermal material collected presents not only new forms, but new facts about old forms and new locality records for others. Most of the new material described was found in the cherty and dolomitic beds of the Fort Atkinson limestone member (Middle Maquoketa). This member was found best exposed at its type locality, the quarry at the old blockhouse near the town of Fort Atkinson in Winneshiek county. Here a large amount of recently quarried rock yielded abundant echinodermal remains. Many fragmentary specimens of undetermined relationships were found. These assure the future student that the field is but partly worked.

The most interesting discovery is a heterosteleian cystid which belongs to a little known race. Its relatives are largely European. It is placed in a new genus, *Iowacystis*, and it does not fit well into any of the defined families. A heterocrinid exhibiting thick and unusually large proximal stem columnals proves to be new and a *Porocrinus* which has undergone much reduction of its fold areas is described and illustrated.

The writers wish to acknowledge the valuable suggestions of Drs. Frank Springer and August F. Foerste to whom photographs were submitted and whose opinions were solicited concerning the new *Ectenocrinus* and *Iowacystis* respectively. The papers of Dr. F. A. Bather have been freely consulted in the study.

¹ Slocum, A. W., and Foerste, August F., New Echinoderms from the Maquoketa Beds of Fayette County, Iowa, Iowa Geol. Surv., vol. XXIX, pp. 315-384, 1924.

CYSTOIDEA von Buch

AMPHORIDEA Haeckel (*pars*)**Anomalocystidæ** Meek*Iowacystis* gen. nov.

Theca triangular, compressed, presumably concavo-convex, surrounded by a border of marginal plates which are extended to form a part of the surface on each side. A single process, or arm, composed of many small ossicles arises from a special group of circum-oral plates near the apex of the convex or oral side. Body plates of the oral side smaller and more numerous than those of the opposite or posterior side where they display bilateral symmetry. Anal pore in sagittal plane at the lower left corner of the oral side.

Stem longer than the theca, tapering, composed of vertical rows of ossicles in which there is a short proximal series of thin columnals changing abruptly to a distal series of alternating polygonal pieces most of which are longer than wide.

This genus exhibits a group of characters which places it close to the family Anomalocystidæ and to which it is provisionally referred. However, the triangular outline of the theca, its stem characters, plate markings and single oral process located outside the sagittal plane are foreign to that family. Foerste suggests further relationship to the Mitrocystidæ or Lagynocystidæ. The genus may eventually be relegated to a new family.

Iowacystis sagittaria gen. nov. et sp. nov.

Plates I, figs. 1-5; II, fig. 1; IV, figs. 1-6; V, figs. 1,2.

The description is based on four specimens and a number of stem fragments. For convenience the four thecas may be referred to as *a*, *b*, *c*, and *d*. Specimen *a* is attached by its concave (posterior) side to a matrix of shaly dolomitic limestone. It is the largest and most nearly complete. The exposed convex (oral) side has been crushed in and the basal and lower marginals are wanting at one corner and disarranged at the other. Specimen *b* is free. Several fractures tend somewhat to destroy the identity of the sutures and the plates of the two sides have been pressed together obscuring the original concavo-convexity; the proximal part of the stem is preserved and the thecal apertures near the apex are well shown. Specimen *c* is the smallest. It was freed from the matrix with some difficulty. Its posterior side is well preserved and shows the bilateral

symmetry and plate markings; the apical region is distorted. Specimen *d* is also free, of normal size, has lost some of the body plates but retains a full centimeter of the stem. It preserves best the plates of the anal pore.

Outline of the theca triangular or sagittate. Base arched gently upward and bearing centrally a re-entrant depression for the reception of the stem. Edges nearly straight, each meeting the base at an angle of approximately 64 degrees; basal corners rounded. Marginals thick and heavy, the lateral ones elongate; they are nine in number and form a frame encircling the theca except where it unites with the stem. There are three marginals on each side, the lower of which forms the corner; between the stem and the lower marginal is a single elongate basal marginal. The ninth plate is the apical marginal and it rests in an angle between the contiguous apical ends of the superior pair of marginals. The peripheral faces of the marginals are conspicuously decorated by an intricate system of ridges and grooves. The median marginals and to a certain extent those above and below them are constricted at their mid-length. In the broad depression thus formed lies a narrow transverse ridge which is a slender continuation of the smoother and less decorated posterior surface of the plate. Each marginal forms a part of the surface on the oral and on the posterior thecal sides but is asymmetrical in that it extends farther over the posterior side than over the oral. The apical plate is pentagonal in outline and protrudes beyond the remainder of the theca; the surface of its posterior face is flat and flush with the faces of the contiguous superior marginals; a smooth linguiform elevated band forms its extreme apical part and extends from the posterior surface, of which it is a continuation, down to the apical edge of plate *G*; a distinct groove flanks each side of this apical band, for the reception of which it is slightly undercut.

The somatic or body plates are fewer in number and larger on the posterior side where they achieve almost perfect bilateral symmetry (see Plate V, fig. 2). They are seven in number and are arranged as follows: one, the largest, is hexagonal in shape, and situated near the center; four others, smaller in size and irregularly polygonal in shape, are arranged in an arch whose ends rest on the basal marginals. The sixth is median in position and just above the stem. It is seven-sided, curved below and its lower border is thickened by a heavy ridge of which there is a lateral continuation in the form of a less prominent ridge on the adjoining basal marginals. This plate

and its opponent on the oral side lie between the proximal ends of the basal marginals; all four apparently contribute to the area of the stem facet. The seventh is also polygonal and lies between the right lower and basal marginals; proximally it abuts against the lower right corner of the four-plate arch and distally it partially supports the anal pore. This small plate is the chief disturbing element in the symmetry of the posterior face. Its position and relations are well shown on specimens *b* and *d*.

On the oral side the somatic plates are fully forty in number. Their exact arrangement on the lower half of the theca is uncertain since on each of the specimens at hand a few of the plates are either lost or misplaced. On specimens *a* and *d* the median plate just above the stem appears to be in place and is much smaller than the opposite plate as seen on the posterior side of *b* and *d*; moreover, it does not bear a ridge along its lower border but a groove, thought to be the edge of the stem facet, is visible beneath its lower edge. The other plates of this side except those of the upper part are small, polygonal, and without symmetry.

Near the apical end of the oral side is a group of three special plates, two large and one small. Close to the right hand edge of the theca and on a level with the superior marginals the common edges of the three plates form an elongate groove which opens below into the theca. Out of this groove and over the opening arises a process composed of several small movable plates apparently in two rows and separated along their outer side to form a longitudinal slit. The total length of this arm-like appendage is unknown but on *b* the portion preserved extends beyond plate *A.M.* (see Plates I, figs. 4, 5; V, fig. 1). The right hand and lowermost plate of the three, here designated *O*, is polygonal and elevated into a thick lip around the lower edge of the oral aperture. Above it and to the left is an equally large irregular plate, here designated *G*. It is separated from *O* and the two small somatic plates by simple and nearly straight sutures, but the line of its contact with the left superior marginal is much crenulated to fit the ridges and depressions of the latter's surface. The plate is heavy and thick and the adapical part of its surface is elevated into a pointed cone directed outward and upward; in the apex of the cone is a small depression, evidently a pore, thought to be the gonopore. The small plate, here called *Y*, lies between the right superior marginal and plates *A.M.*, *G* and *O*; viewed

from the right it is oblong quadrangular in shape and it fits closely about the base of the brachial process.

The anal pore appears to be located close to the sagittal or marginal plane. It is at the lower left hand corner as seen from the oral side and is thus located as far as possible from the intake.² The opening is surrounded by a ring of small polygonal, mostly quadrangular, plates distal to which are two larger plates now closely appressed. The crushed condition of the specimen makes restoration of the pyramid difficult and it is believed that one or more plates have been lost from its apical part.

The stem is composed of two series of columnals, a proximal which is made up of pairs of ossicles which are much wider than long, and a distal series of alternating columnals most of which are longer than wide.

The thin proximal ossicles, although somewhat separated in all the specimens, appear to have fitted into each other much as does a number of nested pans with the extended slightly nodose peripheral edge proximal in position. The most distal ossicle of this series, as seen on *a*, is little more than a ring or band fitting around the tapering proximal extension of the first columnal of the larger series. On the posterior side (specimen *b*) where the basal re-entrant is deeper seven pairs of ossicles are visible; there are but five in view on the oral side. The alternating series of columnals, as seen on *a*, tapers gradually and ends in a number of disorganized small pieces which may or may not have belonged to the stem. In *a* there are seven columnals in place on the right and eight on the left. Each columnal on the right or left is in contact with the two on the opposite side. Proceeding distally the length of the contact border with the opposite upper columnal becomes successively longer for the left hand row and successively shorter for the right hand row. The stem at any point is flattened oval in cross-section. The regularity of the columnals as exhibited by *a* is much less apparent on some stem fragments collected at the type locality (Plate IV, figs. 3-6). In these, at intervals, small, more or less equidimensional ossicles occur singly or in groups. On the posterior side of one specimen (fig. 6) there is a tendency to have three ossicles at the same level in the stem.

The markings of the plates of the posterior side consist of a number of scattered low nodes which exhibit no definite arrangement ex-

² See Bather, F. A., *Paleont. Zeitschr.*, Bd. VII, Heft 1, p. 6, 1925.

cept on plate *A.M.* and on the flanks of the superior marginals where they attain a more or less linear distribution parallel to the sides of the theca. The mosaic of small polygonal plates of the oral side is marked by an abundance of nodes and wavy ridges which have a more or less radial arrangement. The median plate just above the stem partakes of the same general pattern. Plates *O* and *G* have especially strong ridges which are notably prominent on the right half of *G* where they are normal to the suture between *G* and *O*. On the flanks of the apically perforated cone on *G* are a number of tiny pustules which have the appearance of being perforated; their purpose, if functional, is unknown. The elaborate system of grooves and ridges on the marginals and their evident continuity from plate to plate along the periphery of the theca suggest that they may have had a part to play in the economy of the animal other than decoration. The larger columnals of the stem are coarsely granular proximally but distally this disappears to the extent that the lowermost columnals are nearly smooth.

Measurements of the four cotypes are:

	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>
Total length of theca.....	22.0 mm.	22.0 mm.	13.0 mm.	22.7 mm.
Width at base.....	21.0 mm.	20.0 mm.	11.5 mm.	20.5 mm.
Length of median marginal.....	7.6 mm.	8.2 mm.	5.0 mm.	7.9 mm.
Length of plate <i>O</i>	4.5 mm.	4.5 mm.		
Length of plate <i>G</i>	6.0 mm.	6.0 mm.		5.5 mm.
Stem, total length ³	34.0 mm.			
Stem, oral side of				
proximal series	6.0 mm.	7.0 mm.		6.6 mm.
Stem, posterior side of				
proximal series		8.1 mm.		8.4 mm.

Occurrence: In the somewhat shaly and dolomitic beds of the Fort Atkinson limestone (Middle Maquoketa) at the old Fort Atkinson quarry, Winneshiek county, Iowa. Collected by A. O. Thomas and H. S. Ladd. The four specimens are regarded as cotypes and are in the paleontological collections at the University of Iowa. Specimens *a*, *b*, *c*, and *d* are numbered respectively 3525, 3526, 3527, and 3528. The stem fragments are entered as number 3529.

Undetermined cystid plate, *A*.

Plate IV, fig. 7.

A nearly perfect rhomb-bearing plate of callocystine characters was found in the highly fossiliferous zone near the top of the Ma-

³ Stem measurements are of doubtful value since the plates of the proximal series are somewhat separated in the material at hand.

quoketa formation. The plate is small (7.2 x 6. mm.), is five-sided, gently curved in the direction of its greatest dimension, and decorated with vermicular sculpturing. It bears a deep-set half rhomb which is curved or somewhat boomerang-shaped. The border of the depression is sharply elevated and the bordering ridge is higher on the outer than on the inner edge of the pit. There are twenty-two dichopores, nine in the shorter and thirteen in the longer limb of the pit.

Collected by A. O. Thomas from the Maquoketa shale in Sec. 32, Fairfield township, Jackson county, Iowa, where it is associated with *Cornulites sterlingensis*, *Plectambonites sericeus*, *Zygospira* cf. *modesta*, *Calymene gracilis*, and others. The specimen is number 3530.

Miscellaneous cystid plates, *B*, *C*, and *D*.

Plate III, figs. 5, 8, 9.

The first of these is a large plate from the theca of some species of *Pleurocystites* similar to *P. beckeri* Foerste. It preserves well the characteristic markings. Maquoketa shale, upper fossiliferous zone, Stockton, Illinois. Collected by H. S. Ladd.

Specimen *C* is a thin six-sided plate marked by twelve heavy ridges which radiate from the center of the plate, one to each angle and one to the center of each edge. Between the radial lines are fine nodes and vermicular ridges. The inner face is smooth. It evidently corresponds to thecal plate 15 or 16 of *Pleurocystites beckeri* Foerste. Collected from the fossiliferous zone of the upper Maquoketa at Sec. 32, Fairfield township, Jackson county, Iowa, by A. O. Thomas.

Specimen *D* is a plate from the basal circlet of *Pleurocystites clermontensis* Foerste. The lower or basal end is thick and flat and makes up a part of the area for the attachment of the stem. A few strong ridges radiate upward from its lower margin. It appears to correspond with thecal plate 4 according to Bather's system of numbering. Collected by H. S. Ladd; Fort Atkinson member, Fort Atkinson, Iowa.

CRINOIDEA

INADUNATA

FISTULATA

Heterocrinidæ*Ectenocrinus elongatus* sp. nov.

Plate II, figs. 3-8; V, figs. 3, 4.

This species is based on five specimens, four of them free and one attached to a chip of rock. They are here referred to as *a*, *b*, *c*, *d* and *e*. The first three preserve the basals, radials and part of the brachials, *d* preserves the basals and part of the radials, *e* is represented by a number of plates all more or less jumbled. All five preserve large proximal stem segments.

Calyx small, round, elongate, expanding gradually to the top of the radials just above which it becomes slightly constricted. Below the basals are two to five round heavy columnals which become successively narrower and shorter distally until they grade into the normal stem. This unusual feature gives the crinoid a very elongate appearance and a proportionally much wider diameter through the basals than is usual in heterocrinids.

Basals five, pentagonal, sides sub-parallel; the upper sutures which are in contact with the inferradials are longer than those in contact with the base of the undivided radials thus making four of the basals asymmetrical while the fifth which supports the inferradials of the right posterior and right anterior rays is a perfect pentagon. Radials five; the right posterior, the right anterior and the left anterior are compound; the superradials are larger than the inferradials and in direct line over them. The inferradials rest point downward between the basals; they are pentagonal in shape except the right anterior which is hexagonal due to a small suture at its upper left hand corner where it is in contact with the right posterior superradial. The right anterior and left posterior superradials are quadrangular, a little wider above than below; the right posterior is hexagonal due to truncation of opposite corners, one to receive the first anal and the other to make contact with the right anterior inferradial as mentioned above. The suture dividing each compound radial is curved gently downwards. The two undivided radials are the largest plates in the calyx, the anterior one is heptagonal and the left posterior is octagonal, the extra suture in the latter being

due to the position of the anal. Primibrachs two, the first quadrangular, narrowed distally and transversely rounded just above its mid-length; the second shorter, pentangular, wider than long and inclined outward distally. The transverse suture at the base of the first primibrach is wide and located in a deep groove indicating considerable freedom of articulation at this point above which all plates appear to be movable. Plates beyond these unknown except a few displaced brachials at the upper end of *a*. Plates of the whole calyx thick and smooth. Anal plates lost except the first plate in specimen *b* which is so rotated out of its position that its exact shape cannot be determined. Ventral sac unknown.

The stem is extraordinary in that there is a number of thick heavy columnals below the basal circle. These diminish in diameter and in length distally (see Plate V, fig. 3). The suture lines between the columnals are distinct and gently depressed below the surface; moreover the columnals are free along their joint faces as illustrated in *b*, *d* and *e* in which they have partly slipped out of line. The suture lines in *e* show crenelate edges and the exposed parts of the joint faces in *d* and others show the radially disposed crenellæ. The proximal suture at the base of the calyx is slightly indented just below each basal. Distally the diminishing heavier columnals give way to round thin ones of less than one millimeter in thickness. In specimen *e* there are two of these below the fifth heavy segment, then one thicker segment comparable in size to the fifth distal and beyond this another thin segment (Plate V, fig. 3). Beyond this the stem characters are unknown. Whether it continues as a series of thin ossicles or as thin ones alternating with heavier ones must await discovery of new material.

The following measurements taken in millimeters are added:

	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>
Length of stem preserved.....	7.6	6.1	2.4	6.5	5.5
Diameter of largest columnal.....	4.1	3.8	3.0	3.7	3.0
Length of largest columnal.....	3.1	2.9	1.7	2.4	1.6
Length of calyx to top of radials.....	5.0	5.0	4.0	---	---
Diameter of calyx at top of radials.....	5.1	5.0	---	---	---
Length of anterior radial.....	3.0	2.8	---	---	---

Dr. Frank Springer to whom a photograph of this species was submitted writes⁴ that "there is a tendency in some members of the Cincinnati series toward such enlargement. One form called *Heterocrinus juvenis* not only does that but the crown has broken

⁴ Personal communication, April 26, 1925.

off above the basals and then rejuvenated so that we get a crown no larger than the stem."⁵

Occurrence: In the Fort Atkinson limestone (Middle Maquoketa) at Fort Atkinson, Iowa. Collected by A. O. Thomas and H. S. Ladd. The specimens are preserved in the paleontological collections of the University of Iowa. Specimens *a* to *e* are numbered respectively 3771-3775.

Ectenocrinus raymondi Slocum

Pl. II, fig. 2.

1924. *Ectenocrinus raymondi* Slocum, Iowa Geol. Surv., Vol. XXIX, p. 337, pl. XXIX, figs. 5-9.

A fine specimen with six expanded arms lying anterior side uppermost was found attached to a slab of soft shaly dolomitic limestone near Clermont. In general proportions, shape and size of the calyx and stem characters, it is very similar to Slocum's holotype from the same locality. The specimen was removed from the slab and the anal side was uncovered but unfortunately the anal series of plates are lost, and some of the other plates of the posterior side are much displaced.

The five basals are more regularly pentagonal than in the holotype and the complete radials show well the small facets at their basal angles where they meet the neighboring inferradials. Three of the radials are compound and two are complete. The anterior radial is the largest plate in the calyx; superficially it appears to be four-sided but the small edges at the lower angles increase the number of sides to six. The other complete radial is heptagonal due to truncation of its upper right hand corner for the reception of the first anal plate. The three superradials are four-sided except the posterior one which is pentagonal due to position of the anal. Primibrachs two, the first quadrangular, wider than long, the second pentangular, also wider than long. Secundibrachs many, one arm has over thirty; rectangular or wedge-shaped and uniserially arranged. Sides of the plates flat. The outspread position of the arms is advantageous for study but no evidence can be seen of the "shallow, rounded grooves" mentioned by Slocum; slender ramules are present and attached to the ventral side of the arms.

Stem round, tapering, columnals thin.

⁵ For illustration see *H. juvenis* Hall, 24th Rep. New York State Cab. Nat. Hist., 1872, pl. 5, figs. 9, 10. Also 32nd Ann. Rept. Ontario Dept. of Mines, Part IV, p. 10, pl. I, fig. 7, 1925.

Length of stem 3.85 mm.; length of calyx to top of IBr_2 , 8.25 mm.; length of largest arm above IBr_2 , 28.5 mm.

Occurrence: Elgin shaly limestone (part of Lower Maquoketa), Root's farm, 2.5 miles northeast of Clermont, Iowa. Collected by A. O. Thomas. University of Iowa Collection, number 3770.

Cyathocrinidæ

Porocrinus fayettensis Slocom

Plates II, figs. 9-16; IV, fig. 8; V, figs. 6, 7.

1924. *Porocrinus fayettensis* Slocom, Iowa Geol. Surv., Vol. XXIX, p. 333, pl. XXIX, figs. 14-22, pl. XXX, fig. 14.

Four specimens (nos. 3696, 3697a, 3697b, 3699) and some fragments referable to this species were found at the old Fort Atkinson quarry. They preserve more or less of the thin-ossieled tapering stem. Three of them are partly imbedded in a hard matrix but the fourth (no. 3696) is free. It is nearly globular in shape and the ornamenting ridges are sharper and slightly more nodose than on Slocom's paratypes which are at hand for comparison. Moreover, none of the Fort Atkinson specimens show the fine granulations observed by Slocom on his specimens from Clermont and Bloomfield.

One specimen (no. 3693) with decidedly smooth but not ridgeless plates, has prominent transverse ridges on the infrabasals just above the stem-facet and well sunken and somewhat reduced fold-areas. It was found in a road gutter about two miles southeast of Nordness, Winneshiek county. Several loose plates, chiefly radials, were also found here.

Another interesting theca (no. 3692) picked up at this locality is laterally compressed and is decorated with five prominent angular ridges which rise at the lateral infrabasal sutures and pass to the middle of the basals. Here they divide into a Y each upper branch of which extends to an arm-facet above. Other ridges on the thecal plates, except as noted ahead, are much subdued or practically wanting. This ridge pattern divides the surface of the theca into ten polygons, the lower five of which are elongate pentagons, the base of each in turn being an edge of the stem-facet; the five upper polygons are subrhomboidal in shape, their distal angles being rounded and situated between the arm-facets. A light but readily discernible horizontal ridge follows the shortest diagonal of each rhomb and pentagon. Each pentagon and each rhomb encloses two fold-areas except posteriorly where on account of the radial plate one rhomb

and one pentagon have each an additional one making a total of twenty-two. The fold-areas are much less sunken than in typical individuals of this species. As usual in this genus the fold-areas occur at the common corners of three plates and the angle of each plate is bisected by a median fold parallel to which are successively shorter folds extending to the suture. In normal fold-areas the ridges are of equal size and the number of folds on each side of the median is from three to five. In the specimen under discussion only the uppermost and lowermost fold-areas approach normality; the others are peculiar in that the median fold is conspicuously heavy and reaches almost to the center of the plate. The parallel folds are much shorter and reduced to two, one or none, while along the upper edge of the radianal even the heavy median folds are virtually obsolete. The reduction of the folds is most nearly complete along the periphery of the theca especially on the right side but all the fold-areas except the four at the level of the anus exhibit more or less loss. The three strong median ridges separated by 120 degree angles are striking decorations of the theca (see Plate V, fig. 6). Height of specimen, 10.1 mm., anterior diameter, 11.2 mm., lateral diameter, 8.0 mm.

The differences between this specimen and the types of the species are greater than those existing between some of the species of *Porocrinus* but the authors prefer to regard these characters as an individual variation until more material illustrating the same features is found.

Miscellaneous crinoidal remains

In addition to the more complete specimens treated above a quantity of crinoidal fragments consisting mainly of stems and isolated plates has been collected. Some of the parts are readily identified, others belong to unknown species and in some cases more material will be necessary for final determination. Some of the parts found are illustrated on Plate III.

Among the material is a number (figs. 1-4, 6, 7) of isolated plates of *Carabocrinus*, close to *C. slocomi costatus* Foerste. Figure 1 represents a large coarsely ribbed radial which shows well the cuneate areas and the diagonal bordered grooves on either side of the arm-facet; figures 2 and 4 are similar but smaller and less perfect. Figure 3 is a complete radial of *C. slocomi*; under a strong lens it shows very well the fine shagreen mentioned by Foerste. Figures 6 and 7

are typical infrabasals of this genus. All the above were collected by H. S. Ladd; number 1 at Stockton, Illinois (uppermost beds of the Maquoketa), numbers 2 and 4 at Fort Atkinson (Fort Atkinson limestone member) and numbers 6 and 7 at Clermont (Clermont shale member).

Figures 10 and 11 are typical of a number of plates which are thick and heavy centrally and have smooth or slightly nodose surfaces, except along the borders where there is a more or less conspicuous row of nodes or short ridges at right angles to the edges. Collected by A. O. Thomas in road gutters about two and one-half miles southeast of Nordness, Winneshiek county, Iowa (Elgin limestone member).

Figures 12 to 14 are proximal portions of stems bearing the lower plates of the cup. They are fairly common and are thought to belong to the Heterocrinidæ. They were collected by H. S. Ladd, number 12 in the Clermont shale pit near Clermont and number 13 in the upper part of the Elgin member in section 17, Orleans township, Winneshiek county, Iowa.

Figures 15 and 16 are two views of the base of a small delicate crinoid. There are five plates of equal size, curved, smooth, and gradually expanding into a bowl-shaped patina; the plates are flattened below and at their union are excavated for the reception of a small round stem while distally the median border of each plate is produced into an angle. The height of the specimen is 5 mm. and its greatest width is a little over 8 mm. Collected by A. O. Thomas two and one-half miles southeast of Nordness (Elgin member).

Figures 17 to 22 are various parts of crinoid stems. The first is a thin segment of a very small round stem along whose periphery is a series of strong spines. The diameter of the round portion is under 2 mm. Figure 18 is a side view of a thick circular segment whose height is less than its width. Its side-face is convex and there is a slight rebate along the suture line. The surface is marked by fine granules and the joint-face is flat with a small pentapetalous lumen. It may be assigned doubtfully to *Atactocrinus*. Figure 19 is a short piece of a sharply pentagonal stem composed of fourteen segments which alternate in thickness and somewhat in lateral extent. At the angles the rims are produced into sharp points which hook downward. Lumen of stem is large and round. In the latter respect it resembles the stems of certain cystids. Figure 20 is a fragment of a stem 9.4 mm. long and 3.4 mm. in diameter. It is star-shaped in

cross section and the sharp ridges at the angles of the stem are beset at intervals with thornlike points. The segments are very thin there being about 23 in five mm.; the suture-lines are flush and inconspicuous except under a high power lens. The joint-face is marked by delicate marginal crenellæ; lumen pentagonal and relatively large. Figure 21 is an incomplete slender stem 32 mm. in length. It is made up of a series of star-shaped segments with strong heavy points. In the succession of segments the points are so arranged that they form a spiral about the stem. This type of stem is fairly common in the Fort Atkinson member. Figure 22 is a part of the stem of *Dendrocrinus kayi* Slocom. It is pentagonal in cross section and 42 mm. in length. Segments are alternately thick and thin, the thick ones being nodose at the angles. The joint-faces are marked by a distinct pattern of crenellæ which extend from the margin to the small five-sided lumen. Fragments and isolated segments of the stem of this species are common in the marly shales near the top of the Brainard member and are very plentiful at the type locality, Patterson's Springs, near Brainard, Iowa. Numbers 17 and 19 to 22 were collected by H. S. Ladd. Number 17 in Fairfield township, Jackson county (uppermost beds of Maquoketa), number 19 in Orleans township, Winneshiek county (Elgin member), number 20 at Clermont (Clermont member), number 21 at Fort Atkinson (Fort Atkinson member), and number 22 at Patterson's Springs (Brainard member). Number 18 was collected by A. O. Thomas in the road gutters two and one-half miles southeast of Nordness (Elgin member). On Plate IV, figures 9 and 10, are illustrated two views of a crushed specimen preserving a part of the arms and stem. The plates of the lower cup are out of place and some of them are lost. The specimen aids the collector in associating certain stem and arm fragments which occur abundantly in the Ft. Atkinson beds.

A THEORY OF ORIGIN OF SOME LIMESTONE MASSES AND SEPTARIA

A. L. LUGN

Certain lensy "limestone" masses that abound in the Des Moines series of the Coal Measures strata of south central Iowa have been observed by many workers. These masses have been rather indiscriminately called, "limestone boulders", nodules, limestone lenses and septaria. The first term applies to none while the other terms are applicable to some of the masses. It is the purpose here to state a theory of secondary origin, arrived at by the writer during the field investigation and based entirely on field evidence. Subsequent to the field work and after the theory suggested below had taken definite form, the writer in conference with Dr. W. A. Parks of Toronto, Canada, learned that he had observed similar limestone masses in the shales of Ordovician age in Ontario. These he had described in a manuscript which he was preparing and was suggesting an explanation of their origin essentially in accord with the views here presented.¹

Two distinct types of these masses were studied, which for convenience, here only, are designated, type A (strictly limestone lenses) and type B (true septaria). The first type (A) occurs as lensy masses varying from small ovoid bodies a few inches in diameter to large flattened masses several yards in maximum dimensions. The two longer dimensions are oriented parallel to the bedding planes of the shale in which they lie. In the sections where they may be seen, they are confined to definite horizons, commonly only to one. The individual sizes increase as the horizon is traced toward a larger lens of limestone at the same level. These larger platelike lenses have an areal extent of a few acres to a few square miles and are not limited to very definite places in the series. They are of little value in stratigraphy except where their horizons can be accurately re-

¹ Since the preparation of the present manuscript, Dr. Parks' paper, above referred to, has come from the press. It is on "The Stratigraphy and Correlation of the Dundas Formation," in the Thirty-Second Annual Report of the Ontario Department of Mines, Vol. XXXII, part VII, pp. 97-99, 1923. (Published 1925).

lated. This is possible only where exposures are close together. The smaller masses of type A border or fringe the larger lenses. This relation is shown in cross-section in figure 1.

The small masses of this first type are always more prolific in fossil remains than the surrounding shale and in most cases a little less so than the larger lenses. Under the microscope most of the lime carbonate, not occurring as fossil shells, is seen to be crystalline, suggesting that it is a secondary deposit from ground water. It can hardly be recrystallized original calcium carbonate for the original shells are preserved and the crystalline material is confined to the

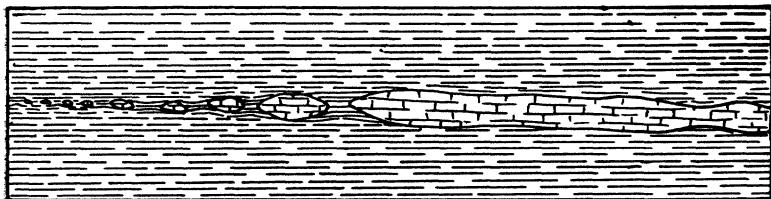


Figure 1. Relationship of the fossiliferous limestone masses to the larger lenses, showing their gradation in size and their occurrence at the same level.

spaces between the fossils and also encloses more or less of the argillaceous sediment. The surrounding shale is quite barren of original fossil remains but in places molds of brachiopod, pelecypod and gastropod shells abound. The lime carbonate of the fossil shells has been removed by solution and now the shale, in most places, is relatively lean in calcium carbonate. The fossiliferous limestone masses and lenses still preserve the original bedding which can be traced into the adjacent shale. The bedding planes bend upward and downward in passing through them. This is shown in figure 2.

It is believed that the masses of type A and many of the larger limestone lenses can be explained on the basis of a secondary concentration of calcium carbonate. The sediment at the time of deposition was highly argillaceous and essentially uniform throughout. Shells of organisms were more or less evenly scattered through the mud. Certain thin zones or limited horizons of small lateral extent may originally have been a little richer in the number of calcareous shells but the deposit as a whole was essentially one of shale-forming material. With subsequent uplift above sea level, the moderately compacted material became subject to the action of ground water.

Calcium carbonate, dissolved from the shale, became concentrated in certain zones, preserving the original fossils and accounting for the secondary calcite which surrounds the shells in these masses and lenses. This process has been of diminishing importance as the material has become more and more compact. The masses and lenses thus preserve the original bedding and very nearly the original thickness of the bed. The bending of the bedding planes on either side of, through and around them is the result of settling and compacting of the enclosing sediment. This volume shrinkage is in part due to the removal of lime carbonate by solution and leaching, leaving only more or less distorted molds of the original fossil shells in the surrounding shale. The abundance of molds of shells in the shale excludes the possibility of the extreme localization of living organisms that has sometimes been assumed for these flat limestone lenses. The present limestone lenses then represent those favorable places or zones where secondary lime carbonate has been precipitated before the enclosed shells had been dissolved.

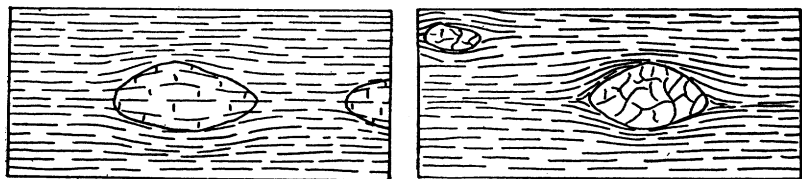


Figure 2. The fossiliferous limestone masses, showing the bending of the bedding planes and their general relation to the enclosing shale.

Figure 3. The septaria, showing their occurrence at different levels and their relation to the surrounding shale.

Masses of the B type are true septaria.² They contain no fossil shells or at least fewer shells than the surrounding shale. The bedding planes of the enclosing shale do not pass through but very clearly bend around them. These masses are made up of about fifty per cent crystalline calcium carbonate and nearly all of the remainder consists of elastic material of textures below $1/64$ mm. This fine material is like that of the surrounding shale. The septaria are not limited to a single horizon, even in a single exposure. The veins of the septaria, which are characteristic of type B, are usually filled

² Grabau, A. W., "Intercretions", *Principles of Stratigraphy*, pp. 719-720, (1913).

with very clear calcite, in some cases with pyrite and in a few a little sphalerite was found.

The complete or nearly complete absence of fossils in the septaria is believed to be due to a nearly complete solution of all fossil shells and a leaching of the shale of its lime carbonate before the secondary concretionary accumulation as septaria began. That these masses are not confined to definite horizons leads to the conclusion that their centers of growth were determined after the local solution and leaching of the primary calcium carbonate had taken place. It is not evident just what determined the position or the beginning of these secondary centers of crystallization. It is evident, however, that with the accumulation of the secondary calcite the surrounding shale is largely pushed out of the way by the force of crystallization. The growing septaria incorporated some of the original sediment now heterogeneously scattered through them. This accounts for the bending of the bedding planes around them and for the absence of bedding within.

If the evidence presented above has been correctly interpreted it is clear that many if not most small masses of limestone that occur in thick and extensive shale formations can be explained without assuming any great changes of sedimentary conditions during the deposition of the formation. Their explanation does not require a shift of land and sea relations, a change of currents, or the assumption of extreme localization of organisms. If a theory of secondary formation can apply to small masses of limestone in great shale formations, as parts of the Des Moines series, may it not within reasonable limits be applied in part to larger, thicker and more extensive strata of limestone throughout the geologic column?

The writer is indebted to Prof. W. A. Parks of Toronto, Canada and to Prof. A. C. Trowbridge of Iowa City, Iowa for encouragement in presenting the above view; and to Prof. A. O. Thomas also of Iowa City for criticisms of the manuscript.

METHODS OF COLLECTING SEDIMENT SAMPLES FROM THE MISSISSIPPI RIVER

A. L. LUGN

(PLATES VII and VIII)

The object of this paper is to describe the methods and procedure employed in collecting samples of sediment from the Mississippi river during the summer of 1925. A few suggestions which occurred to the writer while engaged in the field operation are added. It is not the purpose to discuss the laboratory study of these materials nor to state conclusions.

Various types of sediment samples were taken from Davenport, Iowa, to Cairo, Illinois, a distance of almost exactly five hundred miles as measured along the main channel. The acquisition of these samples was financed in part by the Graduate College of the State University of Iowa and was done under the supervision of Professor A. C. Trowbridge of the Department of Geology. Except for some previous work done by Dr. Trowbridge at the mouths of the river and in the Gulf of Mexico, the present project is the beginning of a comprehensive study of the whole Mississippi river system. It seems proper at this time to present the field methods and procedures employed, since the present work is the first of its kind to be done in a systematic study of any considerable length of a great river.

There are many factors to be considered in an initial undertaking of such a project. A suitable boat or boats must be secured, sampling apparatus must be selected or invented, the types of samples to be collected must be decided upon, a procedure for taking each kind of sample and methods of recording data must be worked out. The spacing and selection of places at which to collect material must also be determined in some systematic way. Most of these things could not be decided before beginning the work as there were no precedents to follow.

A suitable and adequate boat is almost indispensable in making a study of a considerable length of a large river. The writer was very fortunate in securing the boat shown in Plate VIII, owned by Mr. C. E. Delene of Moline, Illinois. Mr. Clovis E. Delene Jr., a student at Augustana college, accompanied the writer as boats-

man and general helper. In these capacities he was efficient and capable in every way.

The Delene was propelled by a stern wheel operated by a Ford engine and could make from five to seven miles an hour in quiet water. In pulling against the current the rate of progress was rather slow but other desirable features outweighed this disadvantage. Some of these features were: length 32 feet over all, beam 8 feet, flat bottom and draft of only 8 to 12 inches. The shallow draft made landing possible at almost any point as well as permitting travel in shoal water. The cabin was commodious and comfortable and with the large space under the forward deck gave ample room for all supplies and equipment. As collected materials accumulated, they were shipped to Iowa City from time to time. The cabin was tightly screened and so constructed as to give complete protection to the occupants from both weather and insects. Every night was spent on the boat and all cooking was done on a portable gasoline camp stove.

A fourteen foot flat-bottomed skiff of the "John-boat" type was towed alongside. This was found to be an essential part of the outfit for it allowed greater mobility and was used in taking almost all of the samples. Such a small boat is also of great value for general use and is a necessity in case of motor or other boat trouble. It can be propelled by an outboard motor or rowed by hand. In the present instance only oars were used but the writer recommends the outboard motor. One man handled the skiff while the other operated the sampling apparatus.

In case an intensive study of a short segment of a large river is to be made, the larger boat may not be so essential since bases of operation can be established at towns or camps and only a small boat with outboard motor need be used. Camp may be moved as often as desired either by car or by boat. This procedure is recommended only where an accessible portion of a river of less than one hundred miles is to be studied in a field season of six to ten weeks. A small river having a shallow channel may be fairly conveniently studied by traveling in a car and many of the samples of sediment can be taken by operating the samplers from bridges, since small streams are usually bridged at short intervals. Travel in this way is faster than by boat and may be of considerable value even on some large streams when a boat is not available. However, the disadvantages are obvious.

Sediment samples were taken which are believed to represent most nearly the river's activity and working capacity at the time of collection. It was decided at the outset to collect material from the bed of the river, from sand and mud bars, from islands as well as suspended *débris*. In time of high water many of the bars are submerged and in such cases "bar" samples are taken as "bottom" samples. At the time the present project was started the river was rising and this continued during the time taken to traverse about one half of the distance covered. A receding stage was experienced during the remainder of the distance to Cairo and low water prevailed during the return trip. This was considered a favorable sequence of water conditions. Most of the samples were taken on the down river part of the trip due to the favorable stage of the water and to the uncertainty in regard to the time required to carry out the project. There is also considerable economy of time in making the collections while going down stream.

One of the essential requirements of bottom samples is that they represent the material being handled by the river at the time collection is made. For this reason samples that represent a vertical section of even a few inches of bottom sediment are likely to be undesirable. Sediment that is scraped from the bed of the river to a depth of less than an inch will best represent the material being handled by the river at that place and time; for the bottom surface at any place is either a site of deposition or of erosion. The methods and apparatus used in taking bottom materials will be described in detail later.

Samples of *débris* from bars and islands were easily taken by hand and preserved in stout cloth bags. The conclusion was reached early in the work that samples of material dredged or pumped from the river's bed might be of great value. Accordingly, gravel and sand samples were secured from commercial dealers wherever possible. In all cases these were taken by hand from the dredge or barge or from the unscreened pile and represented the "river run". Dredged material of this kind is not of quite the same value as the bottom samples but does, in nearly every case, represent the work of the river at its maximum capacity. A "live" gravel or sand bar may be completely removed in a single flood or such a bar of large dimensions may be deposited in one period of high water. A mechanical analysis of gravel or sand from such a deposit gives a composite result and shows nothing of the sorting within the bar. The

greatest value of such samples is that they contain the largest gravels and cobbles, sometimes with diametral dimensions of four to six inches. Such large cobbles are usually of more or less local origin, from nearby tributaries; in all cases they show the effect of stream wear and bear evidence of water handling. The size of such samples was necessarily large in order to represent the various textural grades in proper proportion. They also were preserved in stout cloth bags.

Much can be learned even by a casual study of the sand and gravel piles of commercial dealers. The same type of material can be observed at many places in the levees where these have been built of sediment pumped or dredged from the river in the immediate vicinity. A few "levee" samples were taken. In addition "hand-picked" gravels and cobbles were collected from gravel barges and levees to show the maximum sizes, the degree of rounding, the shapes and the rock and mineral types in the larger grades.

Samples of mechanically suspended matter were taken in order to find out the texture and quantity of solid matter being transported in a known volume of water at different depths at the prevailing stage. These samples were taken in most cases from the main channel where the water was deepest and the velocity greatest. A half gallon of water, with its contained sediment, was secured by an apparatus described below. This was transferred to a half gallon Mason fruit jar and the sediment allowed to settle. After a sufficient time the clear water was siphoned off and the wet sediment was preserved in an air-tight four ounce wide-mouthed bottle. Usually three such half gallon samples of water and suspended sediment were taken at the same place but at different depths; at the surface, at about one foot from the bottom and at an intermediate depth.

The first device used for collecting water samples, with suspended debris, was a common kitchen sink force pump, with three sections of garden hose. One twenty foot and two ten foot lengths of hose were used. The free end was weighted and submerged to the chosen depth and water was pumped into a container. This apparatus is satisfactory in quiet water but is cumbersome and bulky. It can not conveniently be operated from a small skiff. Where there is much current the intake or free end of the hose is carried down stream and its depth becomes uncertain.

The pump was discarded for a simpler and far more satisfactory device, consisting of a weighted half gallon can made of heavy gal-

vanized sheet iron. It is illustrated on Plate VII, figure 3. This can was closed by a one inch cork to which a heavy cord was attached. The whole, filled with air, was lowered into the water on the end of a line to the desired depth and the cork pulled out. The apparatus filled easily and quickly and as the neck and mouth had a relatively small diameter very little interchange of the contents with the surrounding water occurred in raising it to the surface. It was operated from the skiff and to obviate the effect of the current on its depth when submerged the boat was allowed to drift down stream while the can filled. This usually amounted to only a few rods. The total weight of the device is about nine and one-half pounds. The limit of depth at which it was found to work satisfactorily was about forty feet. At greater depths the cork was very hard to pull out against the increased pressure. A heavier can with double or treble the weight of the above should operate at somewhat greater depths.

Another device for taking samples of water and contained sediment at almost any depth likely to be encountered in a river is illustrated in the drawing on Plate VII, figure 4. This is a can, of any suitable volume, similar to the one described above but attached rigidly to a rod two or three times its length. Two adequate weights are also attached to the rod, one at each end and to each of these a line is fastened. The apparatus is lowered by the line attached at B, with the open end of the can directed downward. At the proper depth the line at A is brought taut and the one at B is released thus reversing the can, which allows the air to escape and water to enter. This eliminates the difficulty of removing a cork against water pressure but permits a little error in quantity of contained suspended matter as some water enters as it is being lowered due to the compression of the air in the can as the depth increases. This error increases in direct proportion to the increase of pressure (or depth) but is more or less compensated since the quantity of suspended matter also increases with depth. This device was not put into actual operation.

The "telegraph snapper" bottom sampler was the first apparatus tried for taking material from the river's bed. This device is illustrated on Plate VII, figure 1 (open) and figure 2 (closed). It was weighted and operated at the end of a line in the usual way. A rigid rod would probably be better than a line in quiet and relatively shallow water. It is opened and lowered to the bottom; on strik-

ing the bottom the jaws are spread sufficiently to release the toggle irons which hold them apart and they close around a small quantity of sediment. This sampler is well adapted to taking uniformly fine materials, such as mud and silt when fairly compact, but is unsatisfactory in gravel and even in fine sand. It does not take a sufficient quantity, where the deposit contains particles over a few millimeters in diameter nor does it always close tightly enough, for large grains may be caught in such a way as to hold the jaws partly open. Even grains of sand may hold the jaws far enough apart to allow fine material to be washed out in lifting it to the surface. When the total quantity of heterogeneous material secured is small such losses may be appreciable. The most serious objection to this sampler is that at nearly every trial sand grains worked into the hinges of the toggles and prevented them from completely releasing the jaws. The grains of sand had to be tediously worked out by moving the parts by hand until they operated freely again. It commonly required as many as a dozen trials to secure a single sample. Even had the apparatus worked perfectly, it would have been inadequate because of its small size and the textures of material encountered.

The "Shaw" sampler, suited to taking fine sediment, was also inadequate for collecting gravel and sand. It could not be used except in mud deposits and by the time the project was well under way the sampler designed by the writer and described below rendered its use unnecessary. The Shaw sampler takes "section" samples of small diameter which penetrate the deposit to a depth of several inches and are for that reason, as intimated above, unsatisfactory.

By the time the first thirty miles of the project had been covered, it was plainly evident that the sampling apparatus in hand was entirely inadequate and that something new would have to be designed and made. It should be emphasized that any sampler had to be operated by hand and in most cases from the skiff.

The device illustrated on Plate VII, figures 5, 6, 7 and 8 was designed by the writer and made at a machine shop in Muscatine, Ia. It consists of two weights rigidly attached to a central stem and a loose-fitting cup, which rests around a shoulder on the lower weight. Its total mass is about eleven pounds and its length over all is nineteen and one-half inches. The lower weight was made from a piece of steel shafting three inches long and three inches in diameter. The upper end was turned off, making a shoulder one half inch high and exactly one and fifteen-sixteenths inches in diameter around which

the cup fits loosely. A threaded hole receives the stem in the center of the top of this weight. The lower weight weighs about five and one-half pounds. The stem has a diameter of five-eighths of an inch and is bent into an eye at the upper end. The upper weight is two and one-half inches in length and two inches in diameter and was sawed from a piece of steel shafting. It fits over the stem and is held in place by a rivet. Its lower end is about twelve inches above the top of the shoulder on the lower weight. It weighs about two pounds and the stem an equal amount. The cup was cut from a piece of boiler tubing and is six inches long. It has an inside diameter of exactly two and one-sixteenth inches. This inside diameter is one-eighth inch greater than the diameter of the shoulder on the lower weight around which the cup rests. It is important that the cup should fit neither too tightly nor too loosely around the shoulder. The diametral relations of these parts must be such that the cup can incline easily when the apparatus is prone and settle back again to the vertical position when the sampler is brought upright in lifting it from the bottom. These positions may be seen on Plate VII in figures 8 and 6 respectively. The shoulder must be high enough to prevent the cup from slipping off too easily, in which case the load is lost in raising it from the bottom. This scarcely ever happened. The cup easily slides off the apparatus over the upper weight. This allows other cups of different size and shape to be used interchangeably on the same weight and stem system.

This sampler was operated in most cases from the stern of the skiff. It was lowered to the bottom by means of a stout line; on touching the bottom it inclines to the prone position as shown on Plate VII, figure 8. The skiff was either rowed across the current or allowed to drift with it and the sampler dragged for a short distance. The cup filled with bottom surface sediment usually after being dragged only a few feet. It was then raised to the surface and the contents were emptied into a half-pint Mason fruit jar by lifting the cup off of the shoulder. The first part of this operation is shown on Plate VII, figure 7. The apparatus gave the best results when the amount of line let out was from fifty to one hundred per cent greater than the depth of water. Samples were successfully taken at depths of thirty-five feet with only fifty feet of line.

The sampler described above was very successful and from its first trial was used to take every bottom sample secured between Muscatine, Iowa, and Cairo, Illinois. It takes a distinctly bottom

surface sample and was successful in nearly every instance with the first trial. The quantity of sediment was usually adequate, averaging about six fluid ounces. It worked equally well in mud, sand and fairly coarse gravel, containing a few pebbles up to an inch in diameter. The leakage of fine material was very little, in fact negligible in view of the size of the samples. All bottom samples were preserved in their wet condition in half pint air-tight Mason fruit jars.

A systematic method of procedure to be followed in collecting samples had to be developed early in the work. Obviously bar, commercial and levee samples had to be taken where they were available, so there could be little uniformity in collecting these. Only representative materials were secured from typical and representative bars. Every bar or island could not be sampled nor was it necessary. The determining factors in this collecting of material were local and had to be determined in the field.

Bottom samples were taken in series of from about four to ten at a place and in section across the river at right angles to the channel from bank to bank. These stations, where series of bottom samples were taken, varied from five to twenty miles apart along the river. This spacing was also determined by local factors. In some places the sections were taken where the river was straight and open with no islands or bars exposed above water; in other places where it had many islands and bars. The sections were usually directed from one bank to an island or bar and from there across to the opposite bank. Where the river is divided by an island one side or chute as a rule is relatively narrow and shallow while the other side is wide and deep. The main channel in most cases is through the wider chute. This relation prevails whether the island is associated with a bend in the course of the river or where its course is straight. This procedure of collecting samples was decided upon early in the work and was adhered to throughout. The only modification made was in increasing the average distance between the section stations as the work progressed down the river. Comparable channel samples, taken in the deepest and fastest water, were also secured at irregular intervals between the section stations. Sets of three half gallon water samples, with their suspended sediment, were collected from the main channel at about every fourth or fifth section station. Miscellaneous suspended sediment samples were gotten at numerous other places.

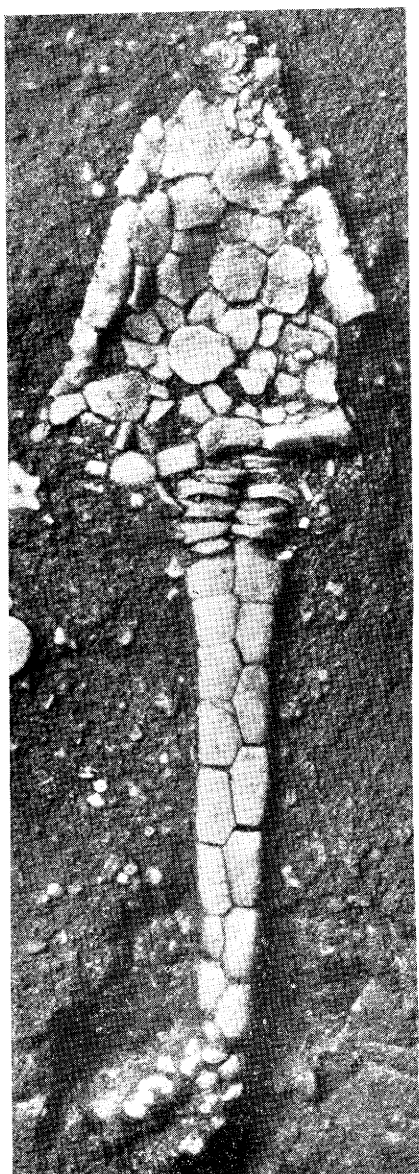
Sections of samples were taken across all of the main tributaries a short distance above their deboucheurs. Missouri River was given especial attention, in that more than the ordinary number of samples were collected about a mile above its mouth. Water with suspended matter was also gotten from some of the tributaries.

The location of every section station or of other individual samples was carefully noted on the large scale charts published by the Mississippi River Commission. A notebook record of depth of water, position relative to islands or bars and the location relative to a located point on the bank was made for every sample. The position of a sample relative to the main channel of the river was also noted. The locations of samples, taken in a section, relative to the starting point were determined by means of a Hymans pocket range-finder (Hymans and Cox, Cambridge). The large boat, the Delene, described above, was tied to the bank or anchored off the point of an island or bar and served as a starting point. The height of the top of the cabin above the water line was known. Using this fixed unit, the distance of any point from the boat could be determined within a few feet or yards. This eliminated the inconvenience of using a stadia rod.

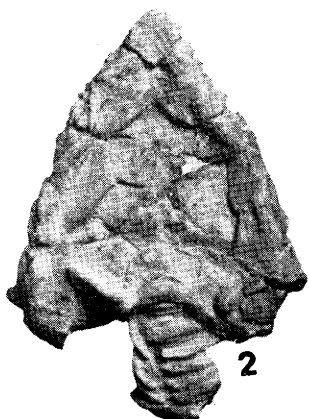
The stage of the water was carefully noted at all gaging stations so that the stage prevailing at the times and places where samples were collected was known quite accurately. The velocity was estimated at many places.

The sediment samples collected from the Mississippi river according to the methods outlined above are being subjected to laboratory studies of texture, shape and lithology.

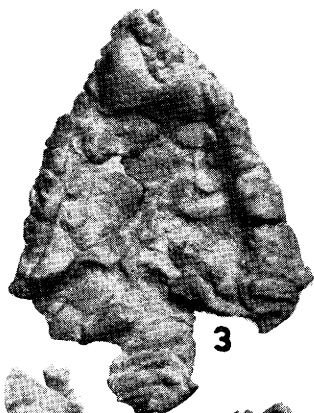
The writer gratefully acknowledges the valuable criticism of this paper by Professor A. O. Thomas of Iowa City, Iowa.



1



2



3



4



5

(For explanations see next page)



PLATE I

	PAGE
<i>Iowacystis sagittaria</i> Thomas and Ladd.....	4
All views on this plate x2.	

Fig. 1. Oral view of cotype *a* attached by posterior side to a rock slab. The plates of the lower part of the theca are partly displaced and the corners are lost. Note the radial markings on the plates, the protruding part of plate *O* at the base of the arm, the length of the median marginal, and the dual nature of the stem. The upper right hand plate of the distal series of stem ossicles shows the contracted part about which fitted the ring-like columnals of the distal part of the nearer series. Specimen number 3525, S. U. I. collection.

Figs. 2-5. Four views of cotype *b*, number 3526, S. U. I.

2. Posterior view showing position of plate *A.M.* and its relation to the other marginals. Note how far the marginals extend over the body surface. Something of the large size and bilateral symmetry of the body plates can be made out. Compare the median plate just above the stem with that in same position on oral side in figure 1.

3. Oral view showing the circumoral group of plates. Many of the smaller somatic plates are lost and the smooth inner surfaces of the plates of the posterior side are exposed. The position of the thick apical group and the relation of these plates to the oral process is shown. Compare amount of stem shown on the two sides.

4. Lateral view, oral face to the right. Note the protruding stump of the oral process and the elevated cone on plate *G*. The upright attitude of plate *A.M.* and the peripheral decorations of the marginals can be seen.

5. Lateral view, oral face to the left. This side shows better the peripheral markings of the marginals.

PLATE II

	PAGE
Fig. 1. <i>Iowacystis sagittaria</i> Thomas and Ladd.....	4
Posterior view of specimen <i>c</i> , x2, S. U. I. 3527. A small specimen attached to the matrix when illustrated. Note the small anal plates at lower right hand corner.	

Fig. 2. <i>Ectenocrinus raymondi</i> Slocum.....	12
Natural size, S. U. I. 3770. Anterior view of a fine specimen attached to the matrix.	

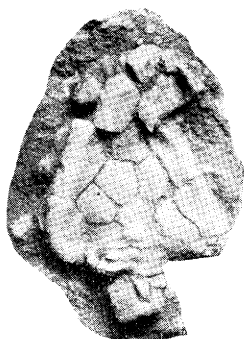
Figs. 3-8. <i>Ectenocrinus elongatus</i> Thomas and Ladd.....	10
---	----

Fig. 3. S. U. I. 3775. A dismembered calyx but with the large proximal stem segments in place. Note how the segments taper distally down to the small ossicles of the normal stem.

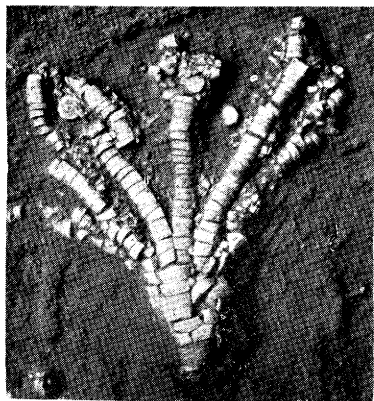
Fig. 4. S. U. I. 3771. Right posterior view of a nearly complete specimen showing compound radials. The proximal stem ossicles are the largest of any in the collection. This is the type, others are cotypes.

Figs. 5, 6. S. U. I. 3772. Right and posterior views of a specimen in which there is a rapid decrease distally in the size of the stem columnals.

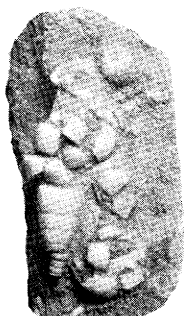
Fig. 7. S. U. I. 3773. Specimen showing partly separated columnals; basals and one or two radials in position.



1



2



3



4



5



6



7



8



9



10



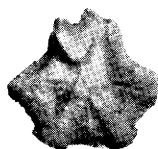
11



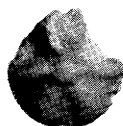
12



13



14



15



16

	PAGE
Fig. 8. S. U. I. 3774. Left anterior view of a small but well preserved calyx having but one large stem segment.	
Figures 3-8 are x2.	
Figs. 9-16. <i>Porocrinus fayettensis</i> Slocom.....	13
Fig. 9. Individual preserving 17.5 mm. of the pentagonal stem, composed of 24 segments. The calyx is partly imbedded in a dense matrix. Natural size. S. U. I. 3697a.	
Figs. 10-13. x2, S. U. I. 3692. Right, left posterior, basal, and left views of a calyx from near Nordness. The first figure shows the reduced fold-areas along the periphery.	
Figs. 14-16. Lot number 3784, S. U. I., x4. Separate radials. Note the elliptical arm-facets, also the markings.	

PLATE III

	PAGE
Figs. 1, 2, 4, 6, 7. <i>Carabocrinus slocomi costatus</i> Foerste.....	14
Fig. 1, 2 and 4. Radial plates x2, showing the costate surfaces; 2 and 4 are partly broken. Figs. 6 and 7 are outer views of infrabasals x4. Fig. 1 is S. U. I. 3790, 2 and 4 are in lot 3875, 6 and 7 are S. U. I. 3792a and b respectively.	
Fig. 3. <i>Carabocrinus slocomi</i> Foerste.....	14
Typical radial plate x2; S. U. I. 3781.	
Figs. 5, 8. <i>Pleurocystites cf. beckeri</i> Foerste.....	9
Fig. 5 is an incomplete thecal plate 11, natural size, S. U. I. 3531. Fig. 8 is thecal plate 15 or 16, x4; S. U. I. 3532.	
Fig. 9. <i>Pleurocystites clermontensis</i> Foerste.....	9
Small plate, probably 4, at the base of the theca, x4; S. U. I. 3533. For this and figure 8 compare illustrations by Foerste on plates 33 and 34, Iowa Geol. Surv., vol. XXIX.	
Figs. 10, 11. Plates of unknown crinoid.....	15
Enlarged x4; S. U. I. 3788.	
Figs. 12-14. <i>Heterocrinus</i> sp. (?).....	15
Fig. 12 is the proximal part of a stem, x4; S. U. I. 3783a. Figs. 13, 14 are two views of the proximal part of a stem preserving the lower plates of the cup, x2; S. U. I. 3777.	
Figs. 15, 16. Base of an unknown crinoid.....	15
Basal and lateral views, x2; S. U. I. 3789.	
Figs. 17-22. Undetermined crinoid stems.....	15
Fig. 17 is a very small segment, x4; S. U. I. 3780. Fig. 18 is a segment, x2, doubtfully referred to <i>Atactocrinus</i> ; S. U. I. 3778. Fig. 19 may be a bit of cystid stem, x2; S. U. I. 3787. Fig. 20 is a piece of thorn-angled stem, x4; S. U. I. 3783b. Fig. 21 a long slender stem, x2; S. U. I. 3786.	
Fig. 22. <i>Dendrocrinus kayi</i> Slocom.....	16
Part of characteristic stem, x2; S. U. I. 3779.	

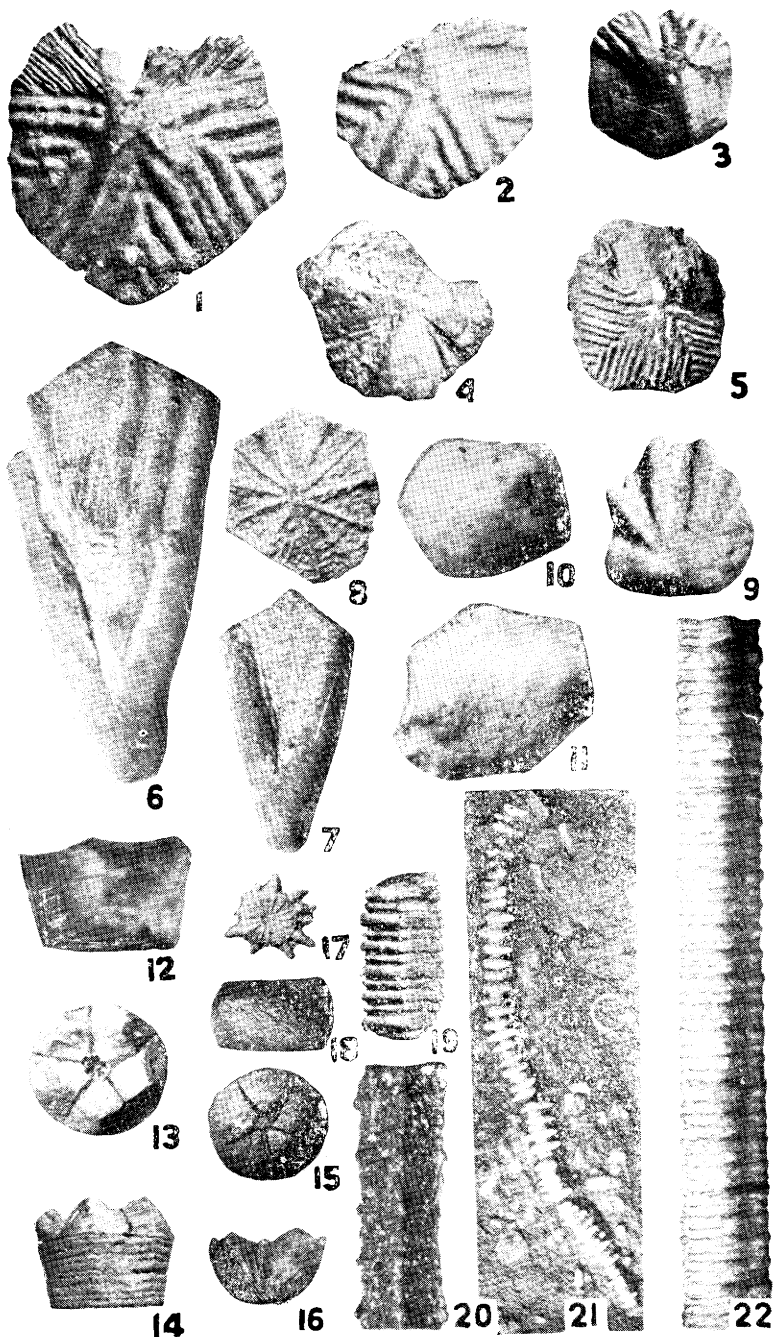


PLATE IV

	PAGE
Figs. 1-6. <i>Iowacystis sagittaria</i> Thomas and Ladd.....	4
Fig. 1. Posterior view of specimen <i>d</i> , S. U. I. collection, no. 3528, x2. A theca preserving the marginal frame. The proximal stem ossicles are much displaced. Anal plates well shown.	
Fig. 2. Oral view of same specimen. Anal plates more or less disorganized. Plate <i>G</i> is in place but plate <i>O</i> is wanting.	
Figs. 3, 4. Oral and posterior sides of a stem broken in two parts, x2. Note the small ossicles set among the longer ones. Compare Plate I, fig 1. S. U. I., 3529.	
Figs. 5, 6. Opposite sides of a piece of stem showing tendency to have three plates at same level, x2. S. U. I., 3529.	
Fig. 7. Rhomb-bearing plate of some unknown cystid, x2. S. U. I. No. 3230	8
Fig. 8. <i>Porocrinus fayettensis</i> Slocum.....	13
Terminal view x2 of a theca showing the star-shaped peristome and the anal opening. S. U. I. No. 3696.	
Figs. 9, 10. Opposite views of an undetermined crinoid from Fort Atkinson. No. 3791. Collected by H. S. Ladd.	
Fig. 11. Base of stem and roots of an unknown crinoid, x2. Fort Atkinson. S. U. I., No. 3793. Collected by H. S. Ladd.	

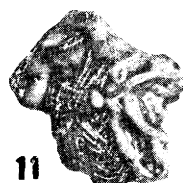
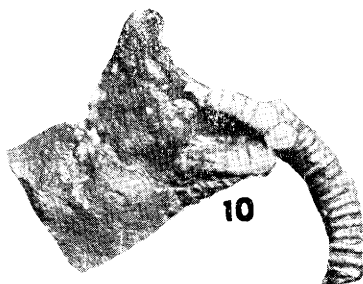
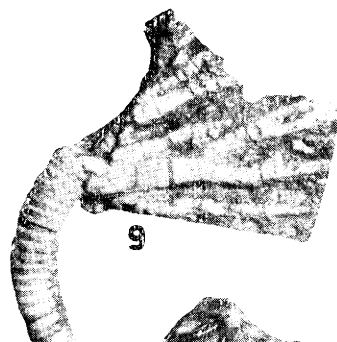
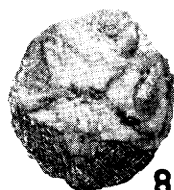
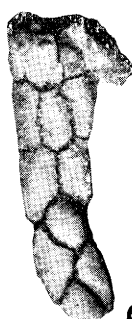
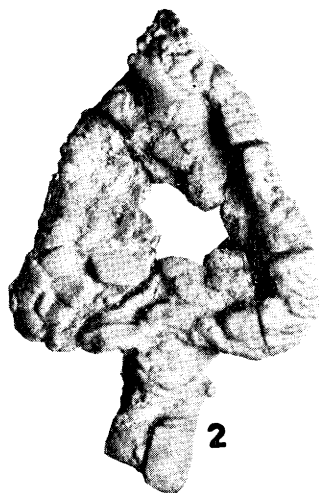
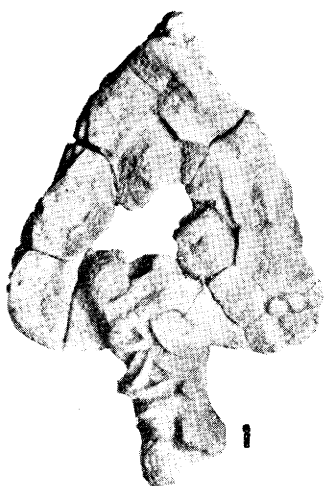


PLATE V

	PAGE
Figs. 1, 2. <i>Iowacystis sagittaria</i> Thomas and Ladd.....	4
Fig. 1. Diagram of oral side, enlarged. Drawn chiefly from specimen <i>b</i>, anal pore from <i>d</i>. <i>Br</i>, brachial process; <i>O</i>, oral plate from which the arm arises; <i>G</i>, gonopore plate bearing a small perforated cone at its upper left-hand corner; <i>Y</i>, a small plate, oblong quadrangular as viewed from the right, bearing a depression in which lower part of the arm rests. Fig. 2. Posterior side showing bilateralism. Drawn chiefly from specimen <i>b</i>, anal pore from <i>d</i>, stem from a separate fragment. <i>A.M.</i> apical marginal; <i>S.M.</i> superior marginal; <i>M.M.</i> median marginal; <i>L.M.</i> lower marginal; <i>B.M.</i> basal marginal. Note that more of the proximal series of stem ossicles are visible from this side.	
Figs. 3, 4. <i>Ectenocrinus elongatus</i> Thomas and Ladd.....	10
Fig. 3. Diagram of large basal columnals grading distally into the normal stem. Enlarged from specimen 3775. Note the uneven proximal edge of the uppermost segment due to the shape of the basals. Compare Plate II, fig. 3. Fig. 4. Analysis of calyx. Note the three divided and the two undivided radials.	
Fig. 5. <i>Porocrinus conicus</i> Billings.	
Analysis after Billings, enlarged (see Geol. Surv. Canada, dec. 4, 1859, p. 34). The anal and radial plates are vertically ruled. The twenty-two fold-areas are inserted at the corners of the plates. Introduced for comparison with fig. 7.	
Figs. 6, 7. <i>Porocrinus fayettensis</i> Slocum.....	13
Fig. 6. From specimen 3692. Diagram of parts of several plates to bring out the reduction of the folds in the peripheral fold-areas and in the upper third of the lower fold-area. Note the vestigial folds, the pentagon and rhombs outlined by the heavy plate ridges and the lighter ridges which bisect each. Sutures are represented by broken lines. Compare Plate II, fig. 10. Fig. 7. Analysis of thecal plates, enlarged. The fold-areas have not been inserted. After specimen number 3692.	

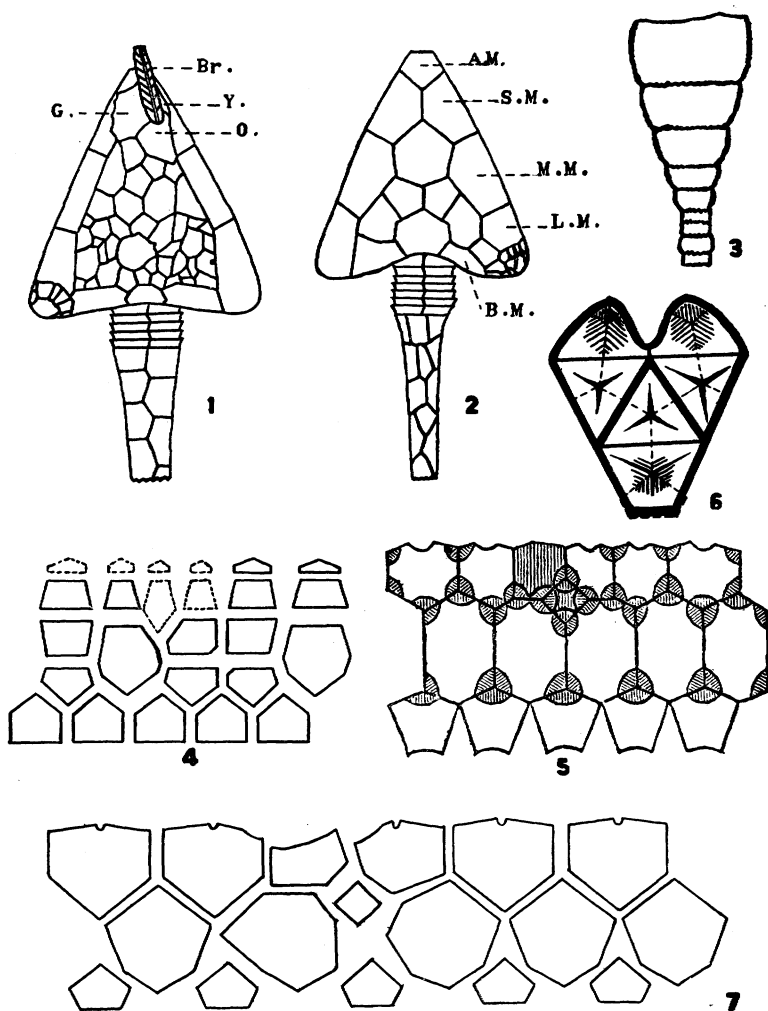
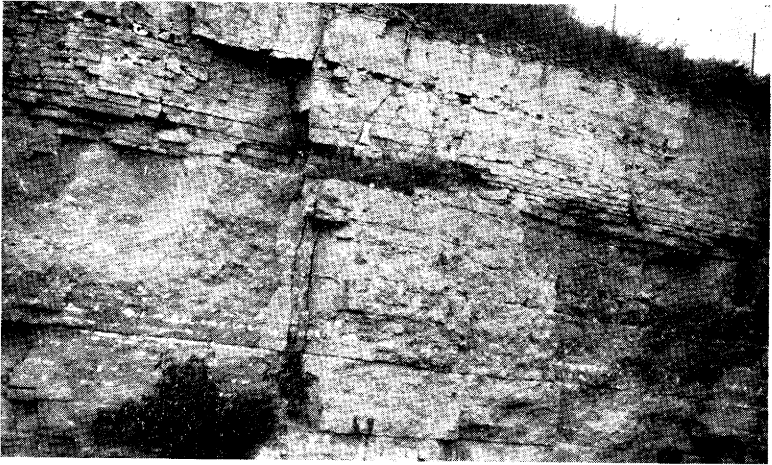
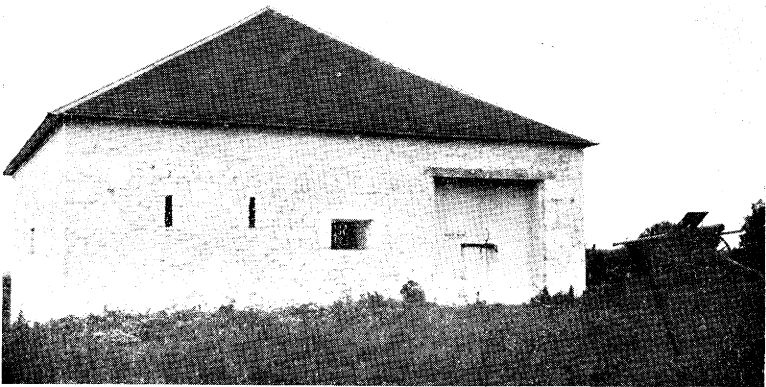


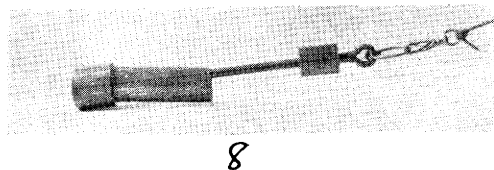
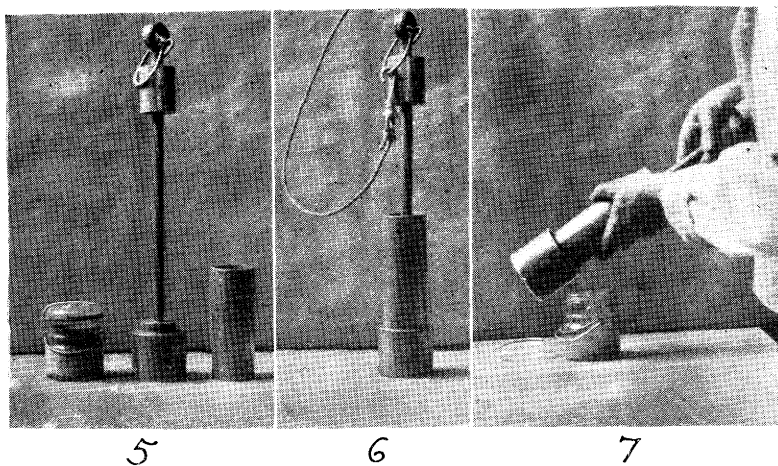
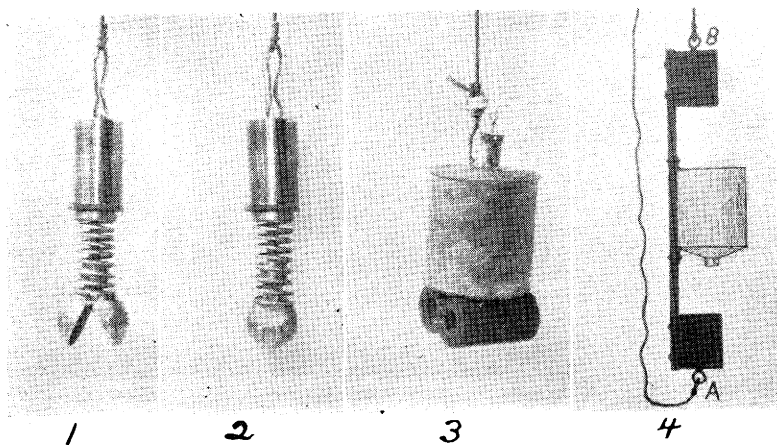
PLATE VI

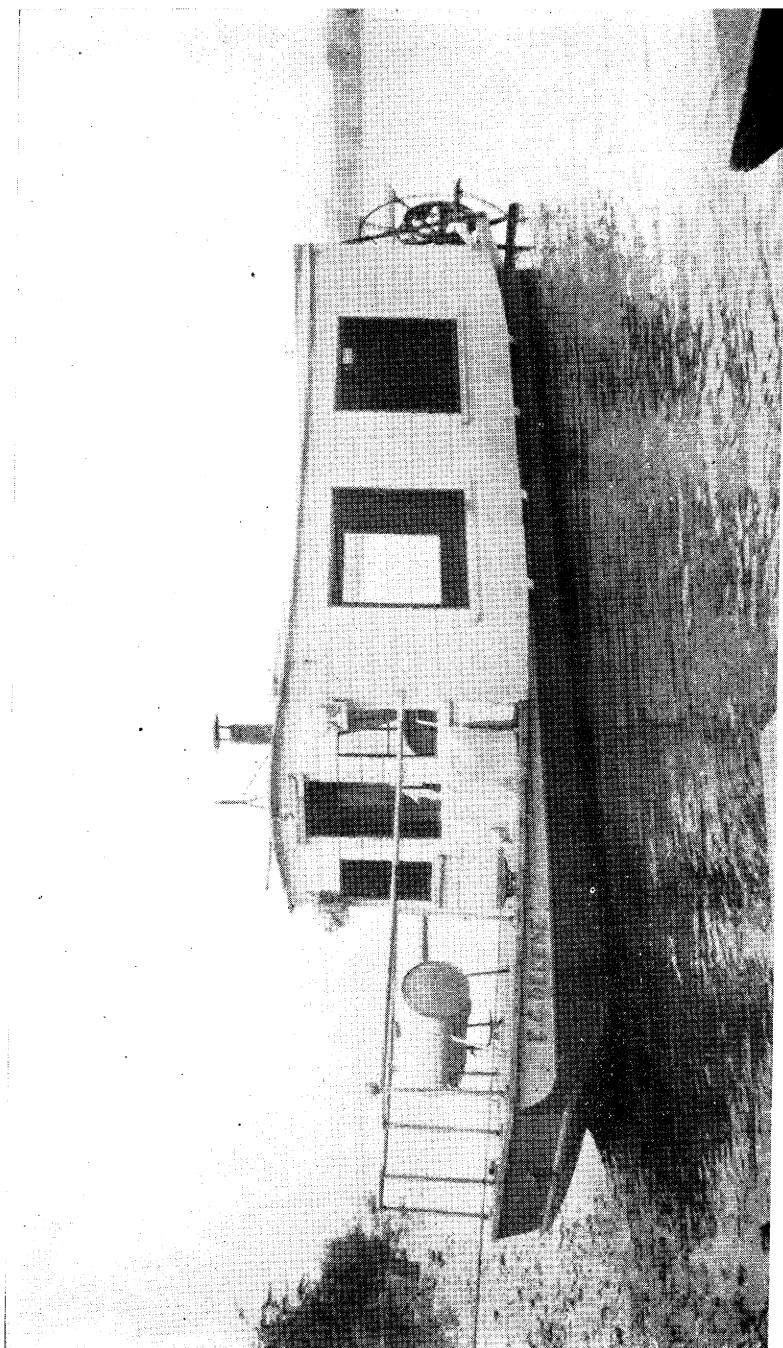


Type exposure of the Fort Atkinson limestone member of the Maquoketa shale. Abandoned quarry near the old blockhouse, Fort Atkinson, Iowa. Note even bedding and chert bands.



Old blockhouse on the hill above the Fort Atkinson quarry. Built in 1840 from stone of the Fort Atkinson member of the Maquoketa. Recently this land was purchased by the State, and the old buildings are being repaired with newly quarried rock.





UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

VOLUME XI

NUMBER 9

FRESH WATER FAUNA OF IOWA

PUBLISHED BY THE UNIVERSITY, IOWA CITY, IOWA

CONTENTS

*A Study of Tritogonia tuberculata, the
Pistol-Grip Mussel*

DAVID T. JONES

*Ecological Studies of the Short-Nosed Gar-Pike
(Lepidosteus platystomus)*

GEORGE E. POTTER

Water Mites of the Okoboji Region

RUTH MARSHALL

A STUDY OF TRITOGONIA TUBERCULATA, THE PISTOL-GRIP MUSSEL

DAVID T. JONES

The incentive to study certain animals comes, not because of their utility, but because their uniqueness arouses curiosity. The blade-beaked skimmers (Rhynchopidae), duck-billed platypus (*Ornithorhynchus*), the dog's head butterfly (*Zerene caesonia*) are familiar examples. Among mollusks, the buckhorn or pistol-grip, *Tritogonia tuberculata* (Barnes), likewise never fails to arouse curiosity. Children wonder "what is the matter with it" and usually regard it as a freak. The noticeable feature about the shell is the surface, studded with protuberances which makes the name "pistol-grip" applicable. Call speaks of the surface as "nodulous," while Baker calls the prominences "tear-like pustules." Simpson¹ regarded this shell as peculiar enough to merit a separate genus *Tritogonia*. Ortmann² thinks it resembles the *Quadrula*s enough in internal anatomy to be called *Quadrula tuberculata* (Barnes). As to the pustulate surface, he calls attention to the fact that *Quadrula lachrymosa* (Lea), the maple-leaf is scarcely less pustulose. Walker,³ however, as late as 1918, is content to let it remain aloof in its own genus *Tritogonia*.

Simpson gives two species and one variety of *Tritogonia* for the United States. In distribution *Tritogonia tuberculata* is confined to the Mississippi Valley and Gulf drainages. Call⁴ gives its range as "Western New York to Minnesota, Iowa and Nebraska; to Kansas and central Texas; to Georgia and Alabama. The species was originally described from Wisconsin." In most older works it goes under the name *Unio tuberculatus* (Barnes), which name dates from 1823.

Economic reports on *Tritogonia tuberculata* for the most part consider it along with other shells. It is used to a certain extent

¹ Synopsis of the Naiades, p. 608.

² Families and Genera of the Najades, p. 254.

³ A Synopsis of the Classification of the Fresh Water Mollusca of North America, p. 45.

⁴ The Unionidae of Arkansas, p. 55.

in the pearl-button industry. Coker⁵ reports it as having "white naere of good texture and quality, but is often spotted. It is thinnish at the tip and has a very rough back; some shells have a pinkish tinge." Baker⁶ reports that the Salt Fork and Sangamon species (Illinois) are of good quality for buttons, and calls attention to the fact that "abnormalities and pearly growths due to injuries or parasitism are rare in specimens of this species examined." Call reports the naere as usually white, but often blotched in large specimens with irregularly distributed, brownish spots. He says that more than half the specimens from the Cahaba River, Alabama, have purple naere.

The following extracts from descriptions bring out the main features of the shell and animal.

Ward and Whipple⁷—"All four gills serving as marsupia. Shell large, solid, rhomboid, truncated posteriorly in the male, elongated with a strong posterior ridge, sexes dissimilar in shape, the posterior region being rounded or subcompressed in the female; hinge complete, surface pustulose, except on the extended portion of the female." Walker—"Epidermis dark olive, hinge plate rather narrow; pseudocardinals strong, rugged; laterals long and straight, near to the pseudocardinals." Simpson—"Well developed lunule filled with epidermal matter. . . . Inner gills much larger than outer, generally free from abdominal sac."

The periostracum is thin and tough, not scaling readily; the prismatic layer thin, and the nacreous layer thick. All three layers enter into the composition of the nodules. On the inside of the shell the naere is smooth showing no conformity to the rough exterior except slight undulations in the posterior region, and an arched furrow corresponding to the umbonal ridge. The latter is sometimes so great as to pull the mantle away from the shell, thus breaking the pallial line as in fig. 3. The nodules are irregular, but often elongate and pointed radially in the opposite direction from the beak. Back of the posterior umbonal ridge especially of the short shells, the nodules are extremely large and united in huge folds.

A good start has been made on the ecology of *Tritogonia tuberculata* in the Fisheries Bureau Report on "Natural History and

⁵ Fresh-water Mussels and Mussel Industries, p. 27.

⁶ Fauna of the Big Vermillion River, p. 33.

⁷ Fresh Water Biology, p. 998.

Propagation of Fresh-Water Mussels⁸." There *Tritogonia tuberculata* is recorded as being found in sand, sand and gravel, gravel, mud and sand, soft mud over firm bottom, mud, and clay and sand. Authorities disagree as to which kind of bottom *Tritogonia tuberculata* prefers, some believing "mud" or "mud over firm bottom", while others believe "gravel". Drew⁹ records it as common, especially on muddy bottoms. Baker found the largest specimens "on a mud bottom although it also lives on sand and gravel bottom." The specimens on which this article is based were brought up by the sand pump from the sand bed in Iowa River just south of Benton Street bridge at Iowa City, Iowa. Somewhere in the neighborhood of fifteen specimens were secured during the period from September through December, 1925. When rock and gravel were pumped up with the sand they seemed to be the most plentiful. They were thrown out very irregularly, more than half the number being secured on two days between which several weeks intervened. As the intake of the sand pump was swinging across the river in ever-lengthening arcs, this would hint at gregariousness. Single specimens were secured while the pumping was confined to the middle of the stream, but the two groups were struck when pumping was approaching shore, yet in deep water and current. Coker, Shira, and co-workers record *Tritogonia tuberculata* as occurring in little or no current, fair or good current, and strong or swift current. Two authorities think it prefers the second situation; one, the last. While *Tritogonia tuberculata* seems to prefer a current, it can live in still water. Of the group on which this article is based, one was kept alive from the latter part of September to the first of the following December in a vessel in which the water was changed once a day or once in two days. *Tritogonia tuberculata* outlived other species (*Quadrula plicata*, *Q. pustulosa*, and *Lampsilis gracilis*) kept under similar conditions. Of the other forms *Quadrula plicata* seemed to approach the endurance of *Tritogonia tuberculata*.

As this study was made in the fall there was no opportunity to observe glochidia for *Tritogonia tuberculata* is a summer breeder.¹⁰ Simpson, quoting Kelly, in "Synopsis of the Najades" says that

⁸ Coker, Shira, Clark, and Howard, p. 106.

⁹ Unios of Iowa, Vol. 2.

¹⁰ Coker and others. Natural History and Propagation of Fresh Water Mussels.

the form with the compressed shell, having the expanded flap behind, is the female. Very little seems to be known of the life history of this species. Coker, Shira, and associates give an illustration of a glochidium, and observed the growth made by a medium sized specimen from July 31, 1911 to Nov. 14, 1913 during which there was an increase in length of 0.36 inch. Baker, in Salt Fork at Homer Park, Ill., found large males 115 mm. long and females 145 mm. long, together with young specimens 46 mm. long.

Tritogonia tuberculata has been and is yet reported as common in regard to numbers throughout its range. In the region of Iowa City the following are the most common mussels in the order of their abundance, judging from what the sand pumps throw up and from the shell piles along the shore.

1. *Quadrula plicata* (*Q. undulata* is less common than *Q. plicata* and is usually not distinguished from it.)
2. *Symphynota complanata*
3. *Lampsilis gracilis*
4. *Lampsilis ligamentina*
5. *Anodonta grandis*
6. *Quadrula pustulosa*
7. *Tritogonia tuberculata*
8. *Lampsilis ventricosa*
9. *Lampsilis anodontoides*
10. *Obliquaria reflexa*
11. *Plagiola donaciformis*
12. *Lampsilis alata*
13. *Quadrula trigona*
14. *Lampsilis capax*
15. *Pleurobema æsopus*
16. *Quadrula coccinea*
17. *Lampsilis recta*—1 live specimen and 1 valve found
18. *Quadrula metanevra*—1 specimen—Coralville
19. *Lampsilis subrostrata*—1 specimen—near Amana
20. *Quadrula ebenus*—1 valve
21. *Quadrula lachrymosa*?—1 valve.

The following living mussels were thrown out of the same sand bed where the specimens of *Tritogonia tuberculata* were secured. These are given in the order of their abundance.

1. *Quadrula plicata*
2. *Lampsilis gracilis*

3. *Anodonta grandis*
4. *Quadrula pustulosa*
5. *Tritogonia tuberculata*
6. *Lampsilis anodontoides*
7. *Quadrula trigona*—1 specimen
8. *Pleurobema æsopus*—1 specimen.
9. *Symphynota complanata*—1 specimen.
10. *Lampsilis recta*—1 specimen.

Shimek's "Keys to the Mollusca of Iowa" were used in classification. Drew's "Unios of Iowa" Vol. 2, Coker's "Freshwater mussels and the mussel industries of the United States" and other articles were used as checks on identification.

I wish to thank Dr. Gilbert L. Houser and Dr. Frank A. Stromsten for the facilities provided in the laboratories of Animal Biology of the State University of Iowa where this study was made, as well as for the helpful suggestions offered.

Tissues for sectioning¹¹ were fixed in Bouin's picro-formol, Carnoy's fluid, Chrom-aceto-formaldehyde,¹² and Chrom-oxalic acid.¹³ The paraffin method for delicate objects was used. All sections were cut 10 micra thick except one thick free-hand section through the edge of the mantle to show the calcareous bodies in the connective tissue. For a detailed study of cell structure it would be better to cut still thinner. Sections through the visceral mass were floated out in warm water immediately after cutting to prevent curling. Delafield's hematoxylin and erythrosin were used as stains, although mucin tests were made with thionin also. The calcareous nature of structures was tested by adding glacial acetic acid to freshly-stained sections and observing changes under the low power of the compound microscope. Permanent sections were cleared in

¹¹ See Guyer for technique unless specifically stated.

¹² Formula used in Laboratories of Animal Biology, S. U. I.

Chromic Acid, 1%	640 cc.
Glacial Acetic	40 cc.
Pure Formaldehyde	320 cc.

1000 cc.

Wash out in water.

¹³ Formula used in Laboratories of Animal Biology, S. U. I.

Oxalic Acid, 8% aq. sol.	800 cc.
95% Alcohol	600 cc.
Chromic Acid, 1% aq. sol.	600 cc.

2000 cc.

Mix in the order as named.

xytol and mounted in balsam. Outlines of drawings of microscopic sections, except figures 8, 9, 14, and 21 were made by the aid of the projecting microscope. Figures 8, 9, and 14 were made under oil immersion.

The ligament in *Tritogonia tuberculata* extends from the beaks posteriorly about half the length of the hinge teeth. It is low, usually not rising above the level of the dorsal part of the valves. Anterior and posterior to the ligament lie the anterior and posterior lunules respectively. The former has more epidermal matter and is better developed. Both lunules and the ligament have a heavy outer layer corresponding to the periostracum of the valves.

The interior of each valve, if normal, is a mirror-image of the other, except for the teeth. The cardinal teeth, normally two in each valve, are large and jagged, the most anterior cardinal in the left valve being usually largest. The broad, smooth, flattened junction between the cardinals and hinge teeth is well developed in both valves. On the right valve it frequently bears a rudimentary third cardinal. There are two hinge teeth in the left valve and one tooth in the right. Of the former, the ventral tooth is usually highest in its posterior extent. The hinge teeth are quite straight but do not run parallel with the dorsal border of the shell.

Both anterior and posterior adductor scars are well impressed, the former being deeper. Continuous with its inner border is the scar of the anterior retractor pedis. The impression of the protractor pedis, immediately posterior to the anterior adductor, is especially deep. The posterior retractor pedis scar, near the dorso-anterior border of the posterior adductor, is very superficial.

The pallial line normally extends from the lower outer portion of the anterior adductor scar around to the outer border of the posterior adductor scar. It does not run parallel to the border, especially in the posterior part, but continues its oval course without following the posterior bulge of the margin. Some mantle vessel, probably the peripheral artery of the mantle, has impressed a groove in the nacre, starting where the pallial line meets the anterior adductor scar, then curving outward and running posteriorly close to and parallel with the margin of the valve. This groove becomes fainter as it proceeds posteriorly. A slight pearly ridge, obliquely dorsal to the depression which corresponds to the umbonal ridge is noticeable in some shells.

The mantle closely invests the inner surface of each valve. It

is attached at the muscle scars by the piercing strands of the muscles, and at the pallial line also by muscular strands. The mantle is thin and barely transparent except the portion distal to the pallial attachment, which forms a thickened muscular edge. The right and left lobes of the mantle are fastened together between the two siphons in the region of the posterior termination of the gills. At the exhalant siphon there is little modification of the mantle, but at the inhalant the margin is much thickened, and the inner part is modified into papillæ, called siphonal tentacles or fimbriæ. These are most robust near the center of the siphonal opening. There are from seven to fourteen large fimbriæ on each side of the siphon and twice that many small ones. The two lobes of the mantle meet near the posterior ends of the hinge teeth. A thickened fold of the mantle (fig. 4x) lying dorsal to the hinge teeth continues as thin sheets over the hinge teeth of both right and left valves. Between the bases of the cardinal teeth the mantle is thickened, and again becomes very thin over the jagged portion of the cardinals.

The function of the mantle in secreting the shell is an interesting study. The edge of the mantle is modified, not only at the inhalant siphon, but to the lesser degree all around. In cross-section it shows an outer, a middle, and an inner lobe (fig. 11). The periostracum is secreted from a groove at the junction of the outer and middle lobes. This groove is lined ventrally by a mound of tall columnar epithelium and dorsally by cuboidal epithelium (fig. 13). The periostracum seems to come off of the latter as a secretion. The cells of this groove are not pigmented as is the neighboring epithelium. This apparatus makes an excellent histological study. Without using a lens the periostracum can be seen stretching over the outer fold to the edge of the valve, in specimens where the mantle has been undisturbed. The origin of the prismatic layer and nacreous layer is not so evident. Since the periostracum is the outer layer, and is laid down first, the other two layers would have to be formed by the outer lobe of the edge or the outer epithelium of the mantle. No histological evidence was found as to the origin of these two. Parker and Haswell make the statement that the prismatic coat is also formed by the edge of the mantle and the nacreous coat by the whole outer surface of the mantle. The outer epithelium consists of tall columnar epithelial cells (fig. 14) resting on a homogeneous basement membrane

under which are the muscle cells and connective tissue. The inner epithelium is similar but contains more mucous cells, many of which are subepithelial (fig. 12). The inner lobe of the edge of the mantle contains much amorphous material which stains blue with hematoxylin. In the middle, connective-tissue layer of the mantle, large masses of granules calcareous in nature were found. These disintegrate least in thick sections.

A process, no less interesting than the activities of the mantle edge, is going forward in the region of the hinge teeth and cardinal teeth. Drew, in "Unios of Iowa", Vol. 1, gives sections through the teeth, showing the undulating layers of nacre deposited by the mantle. Coker and co-workers, in "Natural History and Propagation of Fresh-Water Mussels", say that hypostracum is laid down by the ends of the muscles in place of nacre. Since the muscles retain the same relative position on the shell during the life of the animal they must migrate to keep up with shell growth. Thus a layer of hypostracum extends in a tapering vein through the nacre from the beak to each muscle scar and to the pallial line. Considering the process of enlargement of the teeth by the mantle as going forward over these earlier deposits of hypostracum, the explanation of the growth of this part of the shell becomes as interesting as the marginal growth. It is interesting to note that the thickest part of the mantle, which is in the region of the inhalant siphon, produces the thinnest part of the shell. A fold of the mantle, covering the anterior ends of the gills and the liver, is contained in the umbonal cavity which in *Tritogonia tuberculata* lies under the flattened junction of cardinal and hinge teeth.

The outer gills are attached to the mantle. Keber's organ, a light brown body, lies along the mantle dorsal to the junction. The gills are generally considered as modified folds of the mantle. There are four gills, one pair on each side of the central, visceral mass. The outer gill in *Tritogonia tuberculata* is much shorter than the inner one, as shown in fig. 5. Each gill is composed of two lamellæ with an intervening series of water tubes. The lamellæ are connected by interlamellar junctions between water tubes. Each lamella is finely striated vertically on its outer surface by ridges and grooves. These ridges are the gill filaments. There are ten to the millimeter in one specimen studied. In this specimen, interlamellar junctions showed through the lamella so they could be counted from the outside. There were twelve of these to

one centimeter. Fig. 17 shows a cross section of the dorsal portion of the gills. The filaments cut in section are margined with ciliated epithelium. Spaces, called ostia, open between filaments and communicate with the water tubes. Thus water, admitted through the inhalant siphon, circulates from the mantle cavity through the ostia, through water tubes, to super-branchial chamber, and out at the exhalant siphon. Through the substance of the lamella and interlamellar junctions run many blood vessels. Schwanecke, in 1913, worked out the relations of these vessels in *Anodonta*. He finds that the venous net or reticulum lies vertically near the outer edge of the lamella and extends into each gill filament. The arterial net is represented by a vertical network of vessels near the water tubes. Between these two nets there are connectives. The larger arteries come in through the interlamellar junctions. Supporting rods are found in the filaments. In the dorsal portion of the gill, mucous material was found. Masses of mucous material seem quite common in the mantle and certain parts of the body. Sometimes they are amorphous, sometimes goblet cells, or long subepithelial mucous cells. The last case is best illustrated in the long subepithelial mucous cells in the ventral portion of the foot (fig. 16).

The visceral mass consists of two parts;—the visceral mass proper and the muscular foot which curves over the visceral mass ventrally and anteriorly. The foot in the *Tritogonia tuberculata* is narrower and projects more anteriorly than the foot in mussels of the *Lampsilis* type. A specimen kept in an aquarium quickly buried itself in the sand on the bottom when the water became stagnant, instead of pulling itself over the surface as *Lampsilis gracilis* and *Quadrula plicata* did. The foot in *Tritogonia tuberculata* seems to be very efficient, although it is less frequently protruded than in the *Quadrulas*. Above the foot is the visceral mass proper which in cross-section projects downward in longitudinal midline into the foot (fig. 21). Transverse muscles pass through the visceral mass from the muscles of the foot on one side to those on the other. Most of the visceral mass proper is composed of reproductive organs which give it a spongy appearance. In the visceral mass are imbedded parts of other systems as described below. Dorsal to the visceral mass lie the organs of Bojanus, kidneys or nephridia, two tubes one on each side consisting of a ventral glandular and smooth dorsal portion. They lie just

dorsal to the internal gill and lower, more internal, and more posterior than Keber's organs (fig. 4). A section through the folds of the glandular portion (fig. 15) shows that these folds are made up of a single layer of columnar epithelium, beneath which is a thin layer of connective tissue. Under this are large spaces containing many leucocytes.

Dorsal to the organs of Bojanus, and in midline, is the heart, composed of a tubular ventricle and two flaplike auricles (fig. 4). The ventricle is folded around the rectum, thus enclosing it. The pericardium (fig. 5) covers this organ loosely leaving a large pericardial space.

The nervous system consists of three pairs of ganglia. In *Tritogonia tuberculata* the nervous system is white. In two of the species dissected, namely *Symphynota complanata* and *Pleurobema æsopus*, this system had a salmon colored tinge which set it off markedly from the surrounding tissues and facilitated dissection. In *Tritogonia tuberculata* the cerebral ganglia lie on the ventro-posterior surface of the anterior adductor muscle, the visceral ganglia on the ventral surface of the posterior adductor, and the pedal ganglia in the muscles of the anterior foot region in midline near the junction of the visceral mass proper with the muscles of the foot (fig. 4). The first two pairs are connected by commissures (fig. 21) and the pedal are connected to the cerebral ganglia by commissures. In a cross-section through the pedal ganglia and anterior foot region, the nerve cells were torn apart in sectioning by transparent, elongate capsules, which were themselves shattered by the razor. Some of these contained coarse, granular bodies which stained deep blue with hematoxylin. These parasitic sporocysts (fig. 9) seemed to be confined to the ganglia as the surrounding muscles were free of them. Except for lacking the long flattened tail, they resemble the sporocysts of gregarines which Helen P. Goodrich illustrated in a recent number of the *Quarterly Journal of Microscopical Science*.¹⁴

The labial palps are four in number and lie one pair on each side of the visceral mass. They are joined dorsally for a greater part of their length. The approximated sides of labial palps are furrowed vertically by lateral furrows (figs. 6, 7, and 10). These furrows and the ridges between are lined with columnar, ciliated

¹⁴ *Quarterly Journal of Microscopical Science*. Vol. 69, Part IV, Oct. 1925, Plate 49, page 628, fig. 10.

epithelium which rests on connective tissue. Grooves project into the ridges on either side of the furrows. These grooves are very regularly arranged in *Tritogonia tuberculata*. Many blood vessels run through the connective tissue of the palp. The outer epithelium rests on a heavy basement membrane of homogeneous structure. The labial palps are united and fastened to the visceral mass for about one-half their length as shown in figure 5. However, the labial palps are joined together posterior to this and are attached to the mantle for about five-sixths of their length, the posterior one-sixth being free. In this region, where they are joined to the mantle but not to the visceral mass, there is a distinct dorsal furrow which extends dorsally to the ventral margin of the inner gill. This furrow is lined with columnar epithelium (fig. 8) which has very large cilia. Many goblet cells also occur in this region. The two pairs of labial palps meet at the mouth, thus forming upper and lower lips.

The mouth opening is small. It leads into a short esophagus which gradually enlarges and opens to the right into a sac-like stomach which continues as a blind pouch anteriorly. Both esophagus and the stomach are surrounded by the liver. The intestine leads obliquely, from the ventral part of the stomach, in a U-shaped loop ventro-posteriorly through the mass of reproductive organs to the ventral part of the visceral mass proper, then curving dorsally to the postero-dorsal portion of the visceral mass. This U-shaped portion is sometimes called the crystalline style portion, as under certain conditions it contains the crystalline style. From here the intestine bends sharply on itself, curving to the right and posteriorly. It descends parallel to the ascending ramus of the U until it reaches the most ventral portion of the visceral mass; thence it continues anteriorly along the ventral margin of the visceral mass until under the stomach, then curves sharply on itself, turning to the right and running posteriorly, crossing to the right of the descending ramus of the U. This part is known as the thin-walled portion. After crossing to the right it curves between the two rami of the U as the rectum, and passes into the pericardium and the ventricle of the heart where it takes a horizontal course posteriorly, finally running dorsal to the posterior adductor and terminating in the anus which is bordered by scalloped folds. Starting in the last ascent of the intestine, or in the rectum, is a ventral fold, the typhlosole. The intestine is small in the crystalline style

portion. The thin-walled portion and rectum are much more enlarged. The coiling of the intestine is remarkably uniform in the different species of mussels examined. Variations were noted in *Tritogonia tuberculata* in the anterior extent of the intestine in the ventral portion of the visceral mass, and in the nearness of approach to the stomach of the typhlosolic portion of the rectum (fig. 4).

A cross-section of the rectum in the region of the ventricle (fig. 20) shows an inner lining of ciliated, columnar epithelium with many goblet cells. The typhlosole is composed of connective tissue. The basement membrane of the epithelium is most pronounced here.

The liver, greenish in color, closely surrounds the esophagus and stomach and extends dorsally with the anterior portion of the gills into that fold of the mantle which goes into the beak of the shell (fig. 4). It is a compound tubular gland as shown by cross-section (fig. 18). The larger ducts are lined by folded epithelium composed of slender, ciliated, columnar cells and goblet cells. Some of these folds are caused by actual folding while others are formed by elongation of the cells. The tubes are lined with secreting epithelium, composed of large cuboidal or columnar cells.

Tritogonia tuberculata structurally presents a peculiar shell, some peculiarities of the gills, and a narrower and more anteriorly projecting, blade-like foot than most freshwater mussels. It is hardy, it can endure still water, and is of some economic value. This combination recommends further investigation of its life history from the viewpoint of mussel culture. Dr. Frank A. Stromsten suggests that an investigation of the correlation between lime content of water and type of shell might be well worth while in the transplantation of mussels. It would be interesting to have data from certain parts of Iowa where streams flow over relatively little limestone, and then similar data from limestone regions of our state, and notice the difference in thickness and texture of the shells of mussels from the two areas. Professor Shimek finds snail collecting better in limestone regions than in sand dune areas, even though the latter be wooded. Some similar correlation might be found in mussel distribution. Mr. George Potter brought some mussels from the Okoboji and Little Sioux regions, an area of comparatively little limestone and near the headwaters of the drainage systems. I notice that his specimens of *Symphynota complanata*

are much more fragile than those we find here in the Iowa River. The number of species varies with different localities, and the individuals of one species vary likewise with locality. The whole question is one that calls for data which could be collected easily.

BIBLIOGRAPHY

- Allen, W. R.—1914. The food and feeding habits of freshwater mussels. Biol. Bull., 27, pp. 127-139.
 1921. Studies in the biology of freshwater mussels. Biol. Bull., 40, pp. 210-241.
- Baker, F. C.—1922. The molluscan fauna of the Big Vermillion River, Ill. Ill. Biol. Monog., Vol. 7, No. 2.
- Brück, A.—1914. Die Muskulatur von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 110, S. 481.
- Call, R. E.—1895. A study of the Unionidæ of Arkansas with incidental reference to their distribution in the Mississippi Valley. Trans. Acad. Sci. St. Louis, 7, pp. 1-65, 21 plates.
- Churchill, E. P., and Lewis, S. I.—1923. Food and feeding in freshwater mussels. Bull. Bur. Fish., Vol. 39, p. 439.
- Coker, R. E.—1917. Fresh-water mussels and mussel industries of the U. S. Bull. Bur. Fish., Vol. 36, pp. 11-90.
- Coker, R. E.; Shira, A. F.; Clark, H. W.; and Howard, A. D.—1920. Natural history and propagation of fresh-water mussels. Bull. Bur. Fish., Vol. 37, p. 77.
- De Kay, J. E.—1843. Natural history of New York. Part 5, Mollusca.
- Drew, G.—1890. Unios of Iowa. Vol. 1, Anatomy and histology; Vol. 2, Description of species. Thesis, State University of Iowa. (Not published).
- Edmundson, C. H.—1920. The reformation of the crystalline style in *Mya arenaria* after extraction. Jour. Exp. Zool., Vol. 30, pp. 259-291.
- Fernau, W.—1914. Die Niere von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 110. I Teil, Morphologie der Niere, S. 253; II Teil, Die Histologie der Niere, S. 303; III Teil, Die Nierentätigkeit, Bd. III, S. 569.
- Guthel, F.—1912. Über den Darmcanal und die Mitteldarmdrüse von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 99, S. 445-537.
- Guyer, M. F.—1922. Animal Micrology.
- Hatschek, B., and Cori, C. J.—1896. Elementarcurs der Zootomie. *Anodonta mutabilis* Cless, S. 39.
- Hebers, Karl—1913. Entwicklungsgeschichte von *Anodonta cellensis* Schröt. Zeit. wiss. Zool., Bd. 108, S. 1.
- Howes, G. B.—1885. An atlas of practical elementary biology, p. 61.
 1902. Atlas of practical elementary zootomy. Pl. 20-22.
- Howard, A. D.—1922. Experiments in the culture of fresh-water mussels. Bull. Bur. Fish., Vol. 38, p. 63.

- Huxley, T. H., and Martin, H. N. Revised by Howes, G. B., and Scott, D. H. —1892. A course of elementary instruction in practical biology. The freshwater mussel (*Anodonta cygnea*) p. 20.
- Jaffé, G.—1921. Die Pericardialdrüse von *Anodonta cellensis* (Schröt). Zeitschr. wiss. Zool., Bd. 119, S. 67.
- Kellogg, J. L.—1890. A contribution to our knowledge of the morphology of lamellibranchiate mollusks. Bull. Bur. Fish., 10, p. 389.
- Krug, C.—1922. Morphologie und Histologie des Herzens und Pericards von *Anodonta cellensis*. Zeitschr. wiss. Zool., Bd. 119, S. 155.
- Lee, A. B.—1905. The microtometist's vade-mecum.
- McMurrich, J. P.—1894. Textbook of invertebrate morphology, p. 326.
- Nelson, T. C.—1918. On the origin, nature, and function of the crystalline style of lamellibranchs. Jour. Morph., Vol. 31, pp. 53-111. Has an exhaustive bibliography on the crystalline style.
- Ortmann, A. E.—1912. Notes on the families and genera of the Najades. An. Carnegie Mus., Vol. 8, pp. 222-365.
- Parker, T. J., and Haswell, W. A.—1910. A textbook of zoology, Vol. 1, p. 680.
- Plenk, H.—1925. Zum Bau der Muskelfasern von *Anodonta*. Zeitschr. wiss. Zool., Bd. 125, S. 249.
- Pratt, H. S.—1916. Manual of invertebrates.
- Rassbach, R.—1912. Beiträge zur Kenntnis der Schale und Schalenregeneration von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 103, S. 363.
- Retzius, G.—1892. Das sensible Nervensystem der Mollusken. Biologische Untersuchungen (Stockholm). Neue Folge IV, Tafel IV-VI, S. 11.
- Schneider, K. C.—1902. Lehrbuch der vergleichenden Histologie der Tiere. *Anodonta mutabilis*, S. 536, Litteraturverzeichnis S. 954.
- Schwanecke, H.—1913. Das Blutgefäßssystem von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 107, S. 1.
- Shimek, B.—1915-1918. Keys to the mollusca of Iowa. Appendix to plant geography of the Lake Okoboji region. Bull. Lab. Nat. Hist., S. U. I., Vol. 7, No. 2, p. 75 and p. 80.
- Siebert, W.—1913. Das Körperepithel von *Anodonta cellensis*. Zeitschr. wiss. Zool., Bd. 106, S. 449.
- Simpson, C. T.—1900. Synopsis of the Naiades, or pearly fresh-water mussels. Proc. U. S. Nat. Mus., Vol. 22, pp. 501-1044.
- Splittstoesser, P.—1913. Zur Morphologie des Nervensystems von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 104, S. 388-466.
- Sterki, V.—1907. Note on *Tritogonia tuberculata*. Nautilus, 21, p. 48.
- Vogt, C., und Yung, E.—1888. Lehrbuch der praktischen vergleichenden Anatomie. Blattkiemer—*Anodonta anatina*. Bd. 1, S. 735.
- Walker, B.—1918. A synopsis of the classification of the fresh-water mollusca of North America, north of Mexico. U. of Mich. Mus. of Zool. Misc. Pub., No. 6.
- Ward, H. B., and Whipple, G. C.—1918. Freshwater biology.
- Weisensee, H.—1914. Die Geschlechtsverhältnisse und der Geschlechtsapparat bei *Anodonta*. Zeitschr. wiss. Zool., Bd. 115, S. 262.
- Wetekamp, F.—1914. Bindegewebe und Histologie der Gefäßbahnen von *Anodonta cellensis*. Zeitschr. wiss. Zool., Bd. 112, S. 433-522.

PLATES

PLATE I

Key to figure 1. Elongate form of *Tritogonia tuberculata*

- u. umbo
- u.r. umbonal ridge
- p. pustule
- l.g. line of growth

Key to figure 2. Short form of *Tritogonia tuberculata*

- l. ligament

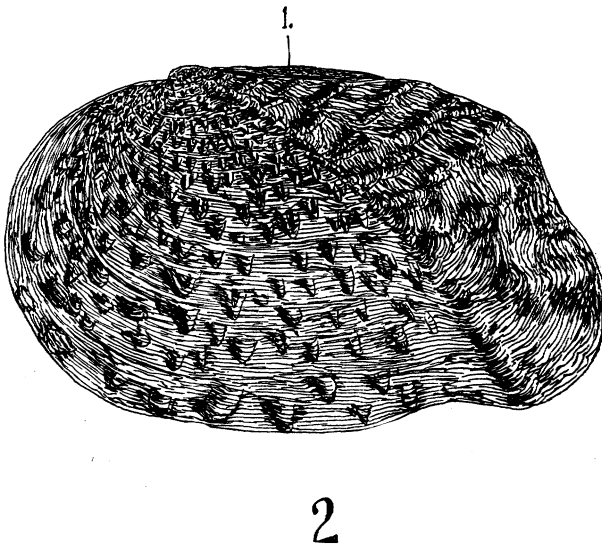
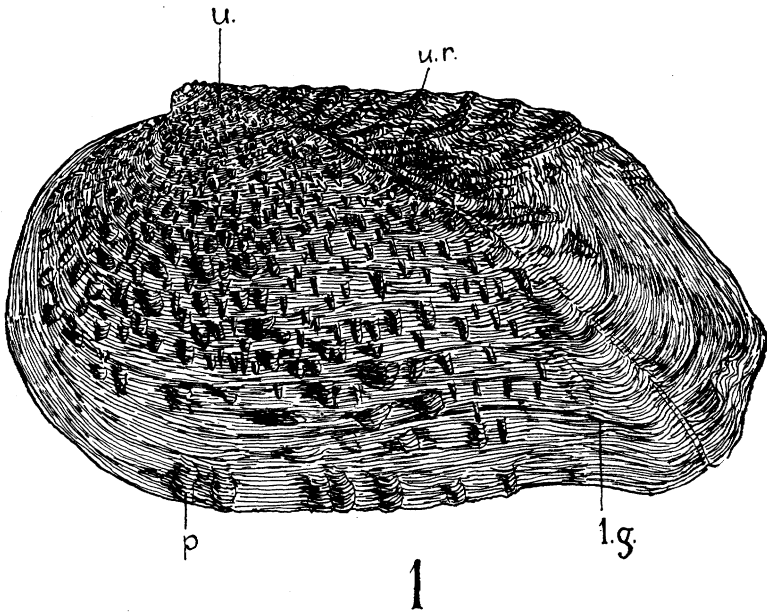


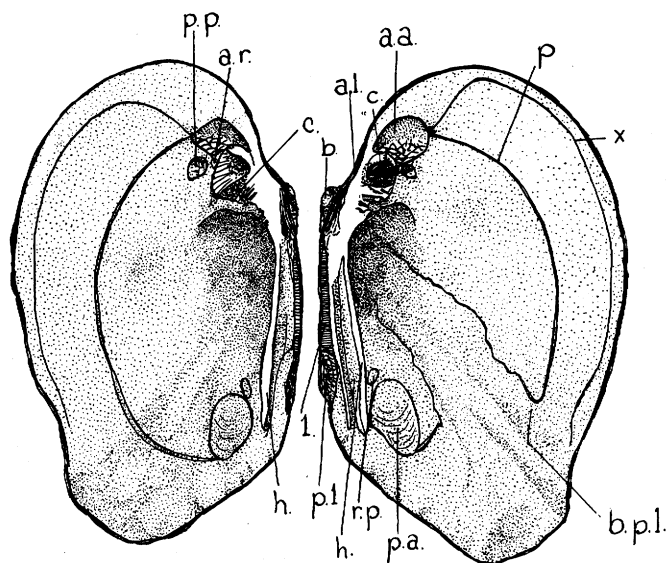
PLATE II

Key to figure 3. Interior of valves. *Tritogonia tuberculata*

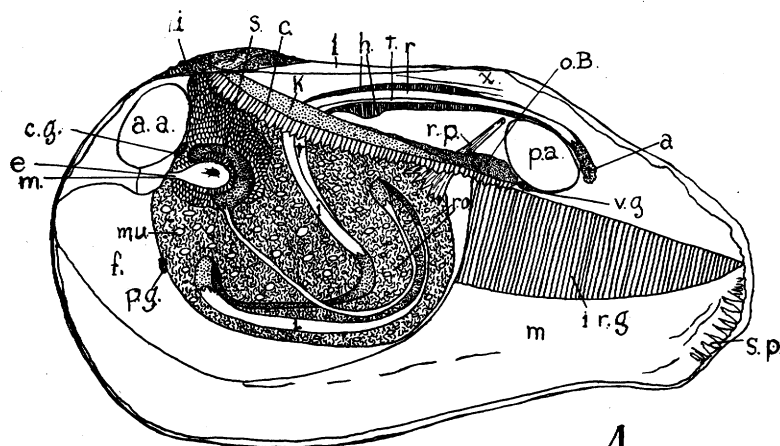
- p. pallial line
- p.p. protractor pedis scar
- a.r. anterior retractor pedis scar
- r.p. posterior retractor pedis scar
- p.a. posterior adductor scar
- a.a. anterior adductor scar
- b.p.l. break in pallial line
- x. groove probably representing peripheral artery of mantle
- l. ligament
- p.l. posterior lunule
- a.l. anterior lunule
- b. beak
- c. cardinal teeth
- h. hinge teeth

Key to figure 4. Conventionalized section through visceral mass in right valve

- li. liver
- a.a. anterior adductor
- r.p. posterior retractor pedis
- p.a. posterior adductor
- s.p. siphonal papilla
- h. heart
- l. ligament
- x. fold of the mantle above the hinge teeth
- e.g. cerebral ganglion
- p.g. pedal ganglion
- v.g. visceral ganglion
- K. Keber's organ
- o.B. organ of Bojanus
- r.o. reproductive organs
- m. mouth
- e. esophagus
- s. stomach
- i. intestine
- t. typhlosole
- r. rectum
- a. anus
- f. foot
- i.r.g. inner right gill
- m. mantle
- c. cut edge of outer left gill
- mu. transverse muscles of visceral mass



3



4

PLATE III

Key to figure 5. Internal structures shown in the right valve. Left valve and left fold of mantle removed

- a.a. anterior adductor muscle in section
- p.a. posterior adductor muscle in section
- p.p. protractor pedis
- r.p.a. anterior retractor pedis
- r.p.p. posterior retractor pedis
- s.b.c. superbranchial chamber
- e.s. exhalant siphon
- i.s. inhalant siphon
- v.m. visceral mass
- f. foot
- s.t. siphonal tentacle or papilla=fimbria
- l. ligament
- b. beak
- i.l.g. inner left gill
- o.l.g. outer left gill
- m. mantle
- a.l. anterior lunule

Key to figure 6. Detail of vertical section of a labial palp

- r. ridge
- g. groove
- e. epithelium
- b.m. basement membrane
- c.t. connective tissue
- e. cilia

Key to figure 7. Detail of vertical section of ventral furrow at junction of labial palps

- v.f. ventral furrow
- l.f. lateral furrows

Key to figure 8. Detail of epithelium from ventral portion of dorsal furrow of labial palps

- b.m. basement membrane
- g. secreting goblet cell
- m. mucous cell
- e. cilia
- w. wandering cell

Key to figure 9. Detail of fragment of pedal ganglia

- n. nerve cells
- p. parasitic sporocysts

PLATE III

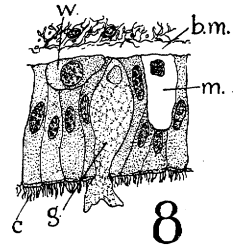
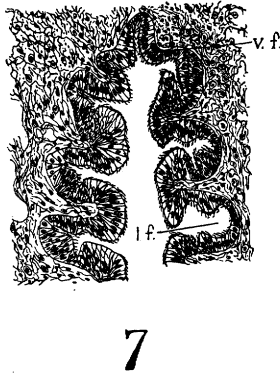
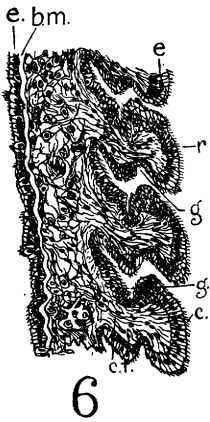
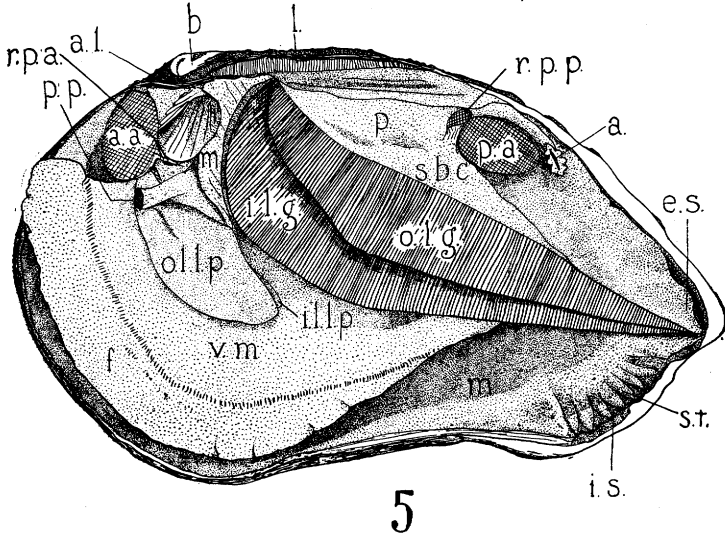


PLATE IV

Key to figure 10. Vertical section through labial palps

- d.f. dorsal furrow
- c.t. connective tissue with cut ends of small bloodvessels
- e. epithelium
- a. labial palp artery
- r. ridge
- g. grooves
- v.f. ventral furrow
- l.f. lateral furrow

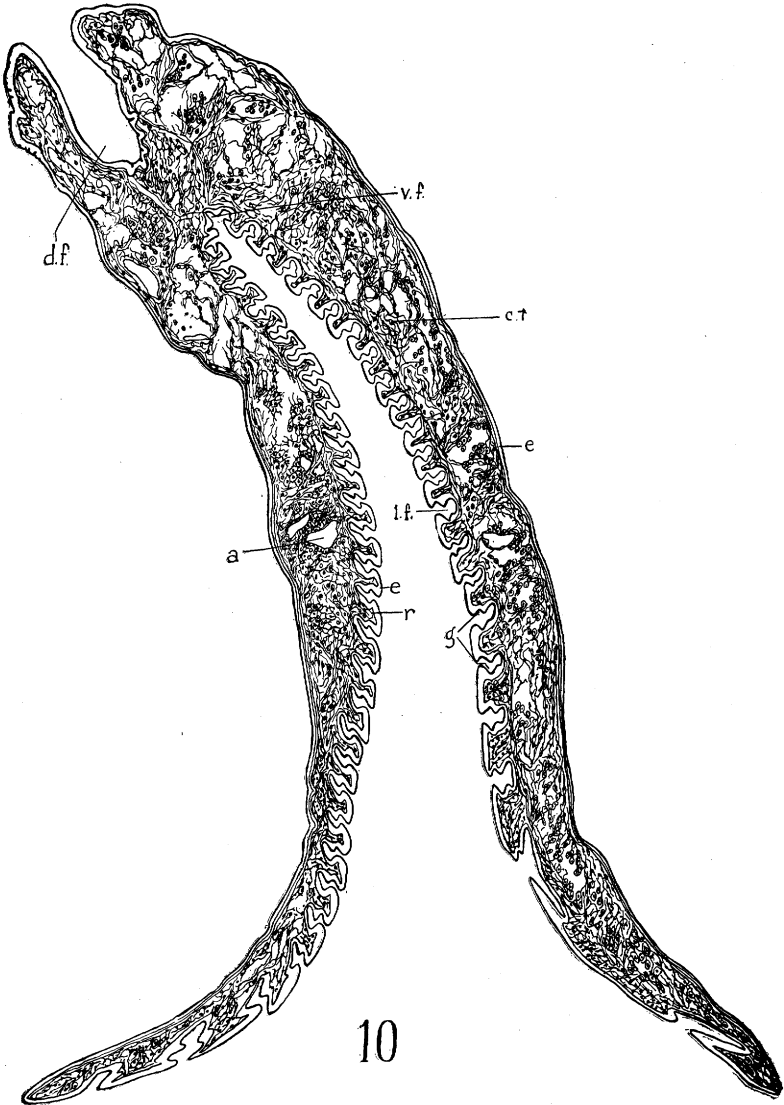


PLATE V

Key to figure 11. Free-hand transverse section through edge of mantle

- o.e. outer epithelium
- c.t. connective tissue layer
- m. muscles
- i.e. inner epithelium
- i.f. inner fold
- s.p. siphonal papilla
- m.f. middle fold
- o.f. outer fold
- p. periostracum
- e. masses of calcareous granules

Key to figure 12. Detail of inner lobe of mantle—10 micra thick

- m. mucous material

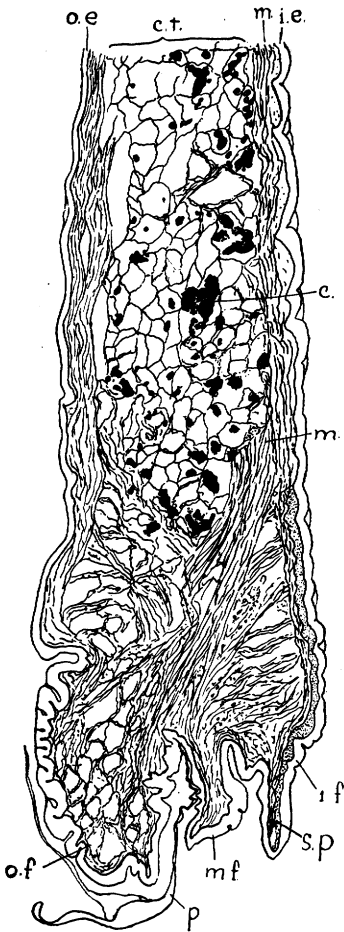
Key to figure 13. Detail of groove secreting periostracum—10 micra thick

- p. periostracum
- pi. pigment in epithelium
- o.f. outer fold
- m.f. middle fold

Key to figure 14. Detail of layers on outer side of mantle. Oil immersion

- e. epithelium
- b.m. basement membrane
- m. muscle cells
- w.c. wandering cells
- c.t. connective tissue
- t.m. transversely cut muscle cells

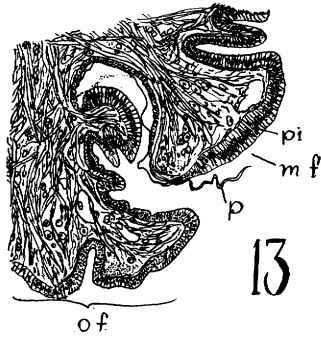
PLATE V



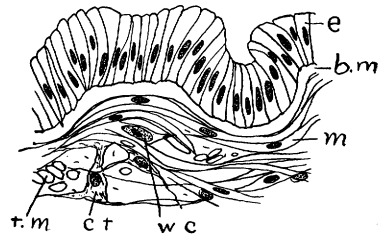
11



12



13



14

PLATE VI

Key to figure 15. Cross-section through folds of the wall of the glandular portion of the organ of Bojanus

- l. leucocyte
- e. epithelium
- c. connective tissue

Key to figure 16. Epithelium of the ventral part of foot

- e. epithelium
- s. sub-epithelial mucous cells
- m. muscles
- c. connective tissue

Key to figure 17. Cross-section through dorsal portion of gills

- a.n. arterial net
- v.n. venous net
- c. connecting vessels between arterial and venous nets
- w.t. water tube
- i.l.j. interlamellar junction
- la. lamina of gill
- i.a. interlamellar artery
- os. ostium
- f. filament
- e. ciliated epithelium
- r. supporting rods
- m. mucous material

PLATE VI

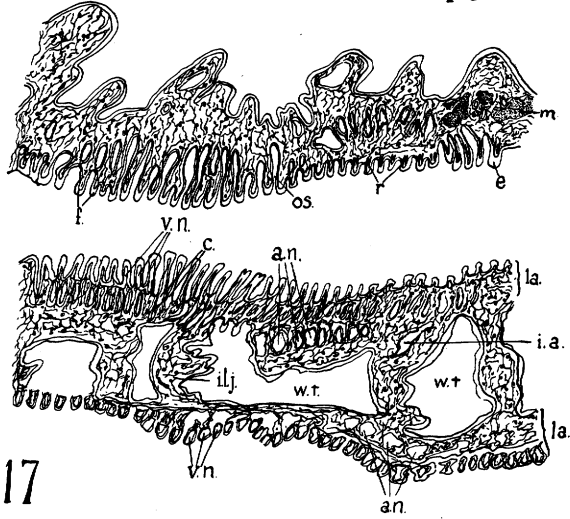
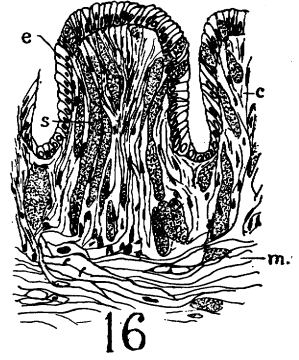
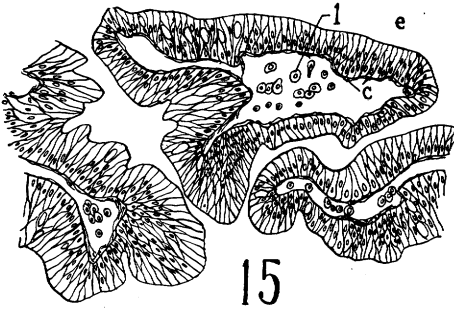


PLATE VII

Key to figure 18. Cross-section through liver

- t. tubules
- d. duct

Key to figure 19. Detail of figure 18

- t. tubule
- d. lumen of duct
- e. ciliated epithelium of duct
- g. goblet cell

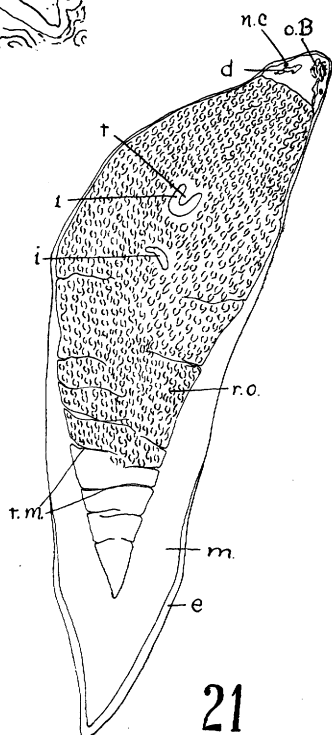
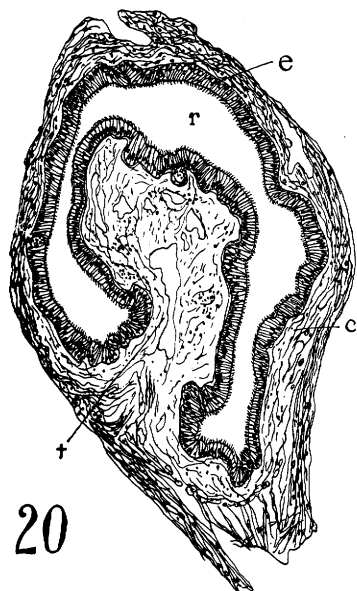
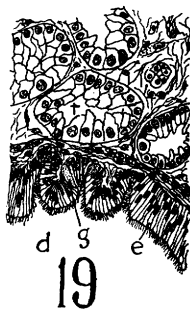
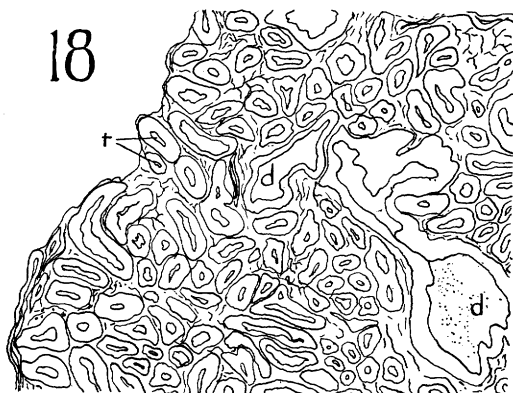
Key to figure 20. Cross-section of rectum in region of the heart

- t. typhlosole
- c. connective tissue
- e. ciliated epithelium
- r. lumen of rectum

Key to figure 21. Conventionalized cross-section through visceral mass

- n.c. nerve commissure
- o.B. cut ducts of glandular portion of organ of Bojanus
- i. intestine
- t. typhlosole
- r.o. reproductive organs
- t.m. transverse muscles of foot and visceral mass
- m. muscles of the foot
- e. folded epithelium and subepithelial mucous cells

PLATE VII



ECOLOGICAL STUDIES OF THE SHORT-NOSED GAR-PIKE (*LEPIDOSTEUS PLATYSTOMUS*)

GEORGE E. POTTER

During the past four summers a study has been made upon the short-nosed gar-pike in the Okoboji Lakes, Dickinson County, Iowa. The work was carried on at the Lakeside Laboratory of the Graduate College, State University of Iowa.

There is a group of seven lakes in the vicinity: West Okoboji, Spirit Lake, East Okoboji, Upper Gar, Middle Gar, Lower Gar, and Center Lake. West Okoboji, where a major part of the work was done, has a length of five and forty-six one hundredths miles, a width of two and eighty-four one hundredths miles, an area of three thousand seven hundred eighty-eight acres, a mean depth of forty feet and a shore line of eighteen and two tenths miles.

In these waters are to be found several fresh water habitats. Some of these are:—(1) the deep water habitat including water from twenty to one hundred and thirty-two feet in depth, (2) the pond-weed or water-plant habitat, found in water from five to twenty feet in depth and (3) the shoal or shore habitat, extending from the shore out to where the water plants become abundant, the depth varying from a few inches to four or five feet. It is in the last two habitats that the short-nosed gar-pikes are most abundantly found in the summer, because it is here that they find their favorite food and resting place. These two above named habitats are particularly extensive in Miller's Bay and Emerson's Bay of West Okoboji and in upper Gar Lake. These areas are indicated by an X on the accompanying map of the region.

Observations were made on the gar-pikes by floating quietly over the water in a row-boat or from standing on the shore. Field glasses were used to good advantage in either case. Specimens were taken for the purpose of examining the stomach content and studying the sexual conditions by two methods; (a) with an ordinary drag-net or seine and (b) by shooting them with a rifle. Gar-pikes have a habit of basking at the surface of the water, in which situation a hunter may slip quite close in a boat, and, with a well aimed shot, kill the fish, or at least detain it until it can be taken

into the boat with a dip-net. A number of the young were taken with the dip-net from the shore.

The gar-pike belongs to the order Holostei and it has been suggested by systematists that this order is in direct line between selachians and amphibians, the teleosts branching from it. The group is divided into several families all of which, except two, are extinct. The Amiidae are represented by the Bow-fin (*Amia calva*) a fish with fusiform body, thin imbricated cycloid scales, and a cellular air-bladder. It is abundant in the waters of North America. The second family is the Lepidosteidae (Gar-pikes) with an elongate body, both of the jaws greatly elongated to form a beak. The maxilla is divided into several segments, both jaws with sharp bony teeth, the tail nearly heterocercal, air-bladder cellular, eyes small, nostrils near the anterior end of the beak, scales rhombic, ganoid and articulated. There is one living genus *Lepidosteus*, whose representatives inhabit the waters of North and Central America. The three common species are; *L. platystomus* or short-nosed gar-pike usually smaller and having a somewhat shorter but broader beak than the following species, *L. osseus* or common long-nosed gar-pike, which has a very long beak (six or seven inches); these two are well distributed throughout the waters of the middle United States while the third, *L. tristychus*, a much larger fish (eight to ten feet) is found in the water of Central America and the Southern United States.

FEEDING HABITS

The gar-pike is quite carnivorous in its food habits, a fact which has considerable bearing upon its status as related to other aquatic animals. The methods used in ascertaining the food habits of this fish have been, (1) to capture them alive, keep them in captivity, and feed them, noting the manner of taking and the different kinds of food that will be accepted; and (2) in other specimens dissect the stomachs and examine the contents as soon as fish are collected. The food of this form proved to be almost entirely animal matter. Occasional small bits of plant tissue were found in the stomachs but, since the amount was always very small and such occurrences rare, it is supposed that they were accidentally taken with other food.

The writer has previously published tables¹ of data on the food

¹ Iowa Academy of Science, Vol. XXX, 1923.

of this animal, so the discussion here will be of a more general nature. Other fish, such as perch (*Perca flavescens*), bluegill sunfish (*Lepomis pallidus*), common sunfish (*Eupomotis gibbosus*), several species of minnows and perhaps others, make up about two thirds of the food material as found in stomach examinations. The other one third was composed of crayfish bodies. In a number of cases there were parts of several such bodies and nothing else.

Stephen A. Forbes, in his paper "Food relations of fresh water fishes" mentions stomach examinations of six specimens in which he found only the bodies of other fish including, hickory shad, black bass and minnows. Forbes and Richardson in their "Fishes of Illinois" state that young gar-pikes will live very well upon mosquito larvæ alone. Mr. H. E. Richardson reports that a sixteen day old specimen had eaten several individuals of a small crustacean, *Scapholeberis mucronata*, nothing else. In another connection he says that the adults in the Illinois river have been seen swimming near the surface and breaking water at intervals to seize emerging gnats and may-flies.

During the warmer weather of the summer months the gar-pike is more active and seems to do most of its feeding in the morning hours, spending the later hours of the day basking in the sun at the surface of the water. The food is captured by grasping it in the toothed jaws. In case the food is another fish it is usually caught with the length of the body across the gar-pike's mouth, which necessitates manipulating it into position so the fish can be swallowed head foremost. The writer has kept live gar-pikes in captivity for long periods of time feeding them every four or five days upon dead sunfish or perch up to five or six inches in length or upon beef liver cut into pieces about one inch square which the animals swallowed whole. The fish have some difficulty in getting the dead objects from the ground to the mouth, but after a trial or two they give the object a quick push with their long jaws and seize it while it is up in the water. It is not uncommon for a gar-pike two feet long to swallow perch that are six inches in length or sunfish that are five inches long.

The food habits, it is seen, are not confined to just one or two species of other animals, but include several, some of which have quite diverse aquatic habits. The gar-pike then, as far as food habits are concerned, has not greatly limited its ecological range in the fresh waters.

GROUND

The ground or lake bottom over which the gars are found varies a great deal. Since they are not primarily ground feeders it does not affect them greatly, except as it influences the habits of the animals upon which they prey. The perch, sunfish and bass generally occur in a more or less vegetated area of mucky or sandy loam bottom. Their food, which is insect larvæ, small crustaceans, plants and some small fish, is found here.

The gar-pike itself eats crayfish and hence it is often seen along sandy or gravelly shores, where these animals abound. The ground seems to be a rather indirect factor in the environment of this fish.

ASSOCIATIONS

All living animals have certain relations with other animals and with plants. Naturally the animal associates of the gar-pike are other aquatic animals, with somewhat similar habits. Many of these are made use of as food, others just seem to happen to be together, while still others have nearly the same food habits as the gar, and compete more or less with it.

These associated animals are so divided and their status given in the following tables.

I. Used by the Gar-pike as Food

Yellow perch	<i>Perca flavescens</i>	Abundant
Pumpkin-seed	<i>Eupomotis gibbosus</i>	Abundant
Bluegill	<i>Lepomis pallidus</i>	Abundant
Green sunfish	<i>Lepomis cyanellus</i>	Rather common
Minnows	Cyprinidæ	Abundant
Black bass ²	<i>Micropterus salmoides</i>	Common
Hickory shad ²	<i>Dorosoma cepedianum</i>	Rare
Crayfish	<i>Cambarus virilis</i>	Abundant
Fly larvæ ³	Diptera	
Damsel fly larvæ ³	Odonata	

II. Accidental Associates

German carp	<i>Cyprinus carpio</i>	Abundant
Common sucker	<i>Catostomus commersoni</i>	Rare
Bullhead	<i>Ameiurus nebulosus</i>	Common
Leopard Frog	<i>Rana pipiens</i>	Common
Bell's turtle	<i>Chrysemys m. belli</i>	Abundant
Snapping turtle	<i>Chelydra serpentina</i>	Common

² Forbes in "Food Relations of Fresh Water Fishes."

³ Pearse in "The Food of the Shore Fishes of Certain Wisconsin Lakes."

III. Those of Similar Food Habits

Black bass	<i>Micropterus salmoides</i>	Common
Rock bass	<i>Ambloplites rupestris</i>	Rare
Bullhead	<i>Ameiurus nebulosus</i>	Common
Wall-eyed pike	<i>Stizostedion vitreum</i>	Rare
Common pike	<i>Esox lucius</i>	Rare

In the first table it is noticed that the perch, sunfish, bluegill and crayfish are abundant in the regions where the gar-pike are found. The rule is quite consistent that if a gar is in a community at least some of the others mentioned will be there also. The group of accidental associates may be brought into the same society by their food habits, for protection, or to reproduce. All of these activities may be somewhat different from the corresponding habits of the gar-pike. For instance the carp is a ground feeder, but in an area where there are water plants, there is much food for it. Other species come to these regions because the plants afford protection for both adult and young. There is a number of other animals whose food consists of the same material as that of the fish listed. The search for their favorite food therefore brings them into association with the gar-pike.

PLANT ASSOCIATIONS

In the portion of the lakes where the gar-pikes congregate and are nearly always to be found, certain water plants usually occur. The most important of these is *Ceratophyllum demersum*, a long slender-stemmed plant, often many feet from one extremity to the other. This weed grows to form a very dense mass, much of which is at the surface, where it spreads out forming an even, green mat. Among the *Ceratophyllum* in the shallower water is often found *Myriophyllum*, a somewhat similar plant. Still another plant which occurs in the habitat of the gar, is *Potamogeton* of several species. On the bottom in some places there is a great deal of *Chara*. Numerous kinds of algæ are found throughout the water.

The dense growth of plants affords food and protection for many fish, small crustaceans, molluscs and larvæ of insects. Therefore they will be attracted here. The gars come here in search of these animals for food, for the direct protection the plants offer, and for a suitable place to breed.

TOLERANCE TO ENVIRONMENTAL CONDITIONS

This animal is able to tolerate many severe conditions which are fatal to most other species of fish in a very short time. The writer once found a gar-pike trapped in an old fish cage. Either the animal was able to get into the cage at a time when the water level was higher (as it had been a month before) and was unable to get out, or someone had placed the animal there. At any rate it was held captive and the water had lowered until most of its back projected out of the small amount of very muddy water in the puddle. There was a small connection of water between that in the cage and the main lake. The oxygen supply of the little puddle must have been nearly negligible but the fish was able to survive without much apparent discomfort.

Following this incident, some experiments were made in view of getting a definite idea of the fish's tolerance in this respect. A live gar-pike was placed in a vessel containing five gallons of water that tested 8 cc. of oxygen per liter (Winkler method). The vessel was covered with screen, but with some space between the screen and the water. At the end of twenty-four hours the water was again tested for oxygen and this time the test was 1.9 cc. per liter. The fish was still alive and apparently not suffering in the least. At the end of twenty days, after the water had become extremely foul, the fish died. The water was tested for oxygen several times during this period and the amount present always corresponded very closely to the amount found at the end of the first twenty-four hours. The test has been repeated a number of times and the results coincide. It was noticed that almost continually during the experiment, the fish would come to the surface at intervals of several minutes and gasp in air. This same action has been noticed by the writer and others when the gar-pike is in natural waters where the oxygen content is low. From this it seems quite evident that the gar-pike has other means of respiration besides the gills. It has been stated by others that this animal uses the air-bladder as a respiratory organ, but the writer, not having completed experiments to determine which organ does the respiring in this case, is not ready as yet to make a statement. The bullhead (*Ameiurus nebulosus*) and bow-fin (*Amia calva*) are probably its closest rivals in respect to tolerance of low oxygen supply, while perch and sunfish will die in a few minutes under the same conditions.

The gar-pike has great endurance in respect to rough handling when compared to many other fish, such as the perch, sunfish, bass, or minnows, many of which will succumb from simply being dragged ashore in a net. The heavy armor of scales offers very good protection from injuries by physical contact.

This ability to endure severe conditions along with the gar-pike's predaceous habits, strong swimming powers and its natural protective coat of armor-like ganoid scales have probably been responsible for its long, successful existence. These factors, no doubt, also have a bearing upon the abundant numbers of these fish to be found in some localities.

ECONOMIC IMPORTANCE

The gar-pike is a branded fish and has a wide-spread reputation for being a worthless nuisance. Since it is predaceous and a voracious feeder, the gar is very destructive to other fish. In Lake Okoboji its principle food is perch and sunfish and it is reported that black bass have been found in its stomach. These fish are all used as food and game by man, so he begrudges the gar-pike the large number that it captures.

The fact that the gar-pike feeds upon crayfish, minnows and a few insect larvæ is a second charge against it. Since the rock bass, black bass, pickerel, and others which are valuable food fish make use of these for food, the large amount of this sort of food consumed by the gar-pike only subtracts from the supply for these more valuable species. Many nets and other fishing tackle are destroyed each year by these strong fish. It is reported by the U. S. Bureau of Fisheries that in Carolina the nets of the commercial shad fisheries often become loaded with gars, nearly to the exclusion of the marketable fish. At the same time the nets are frequently torn by the active struggle of the gars.

The fleshy part of the upper sides or "loin" of this fish has been used for food by Indians, but usually white people have not been able to rid it of the strong fishy taste and odor. However after being soaked in brine over night and well baked the meat is fairly palatable. It is reported that in the Mississippi river the gars serve as host for glochidia of the Yellow Sand Shell Clam (*Lampsilis anodontoides*), an important button producer. Little else can be said in favor of the fish. It is the enemy of most other fishes at some stage of their lives and with its strong swimming

powers, adaptability and other natural protection, it is quite safe from other aquatic animals and conditions. As yet no satisfactory way has been devised for clearing our waters of them, if that is desirable. However it has become customary among fishermen upon catching them, to either throw them out on the shore to die or to break their heads from their bodies.

LIFE HISTORY

As has been shown, this fish has a rather characteristic life career. It is endowed with means for leading a very predaceous life, and with ability to protect itself from enemies, as well as having a fairly rapid rate of reproduction, so it is able to perpetuate its kind quite successfully. The seasonal cycle is about as follows. During the summer, June, July, and August, many of these animals come into the shallow bays, Little Miller's and Little Emerson's in West Okoboji, where they feed upon smaller fish and spend a great deal of time basking in the sun on warm days. Then about the end of August they begin to be less abundant in these shallow bays, making their way to the deeper water for the winter. Fishermen of this region say that they have seen gars through holes in the ice. They will move along quite near the ice, passing across the open hole, apparently not afraid of a man who is moving about. Their movements under the ice seem quite aimless. The low temperature, slowing up the metabolism, is more than likely responsible for this semi-coma, since the writer has kept live specimens through the winter months in tanks at a temperature of seventy degrees F., with no such results.

The time of spawning is quite irregular with the gar. The weather conditions seem to cause some general variations, that is, if the temperature remains low until late in the spring, the general spawning season for the animal will be a little later. There is much variation in the time of spawning among individuals, some spawning as late as July. Several were seen apparently spawning on May twentieth, in the south end of Lower Gar Lake. These were the first to be observed spawning that season (1923).

The water in the lower end of Lower Gar Lake is quite shallow, in fact that part of the lake is no more than a slough. It is here, in this shallow water where there are some weeds to which the eggs may attach, that the spawning occurs. Sometimes one animal, supposed to be a female, is attended by two or more others, presumed to be males, but occasionally they swim in pairs. There is

a great deal of rubbing back and forth along the sides of the female as they all move repeatedly over the same ground. Suddenly the female slaps her tail out of the water with a splash and the fish are gone from the spot.

The eggs are deposited in small masses, held together by a clear gelatinous substance, which attaches to the weeds or even to the lake bottom. The individual eggs are about the size of buck-shot, or 3.5 mm. in diameter, and are dirty-yellowish in color. Their appearance is different, perhaps, from that of any other egg. Under favorable conditions Mr. R. E. Richardson has found that the eggs will hatch in eight days. The young fish are very slender and carry a yolk sac attached to their ventral side. They remain in this condition about seven days when the yolk sac is entirely absorbed. This period when the young gar is carrying the large yolk sac is the most helpless part of its whole life. As soon as the sac is absorbed the fish is a very slender, active animal. It is slaty gray in color at this time and marked with a broad lateral line of black.

During this time the principal food is probably Entomostraca and mosquito larvæ. But very soon they start their predaceous habit of preying on other fish. Forbes and Richardson make mention of a specimen an inch and a quarter long which had taken a minute fish, and another two inches long and only an eighth of an inch in depth had filled itself with no less than sixteen very young minnows. These young gars stay in the shallow water, and at Okoboji in an artificial canal among the water plants, until fall when they go to deeper water with the adults. About fifteen of the fish, varying in length from two and one half to five inches, were taken in the above mentioned canal in August by dipping them up in a net from the shore. The fry and fingerling are very seldom seen because of their slender build, grayish color, shy habits and quick actions. Those which have been found were solitary near the shore, usually among plants and over a muddy bottom. In this way the young animals are afforded very effective protection. They attain a length of four to six inches the first summer, so as a rule the smallest gars seen are at least this large. Their growth is slightly slower the second season and the animals become bolder.

The specimens seen, which were supposed to be spawning, were all at least fifteen inches or more in length which is larger than

the second year animal, so it is likely that reproduction does not begin until after the second year. They are very prolific, the mature ovaries of a large female often weighing more than a pound. Dr. Evermann reports that a female weighing nine pounds, contained, by actual count, 36,460 eggs. It is, then, evident that there is opportunity for rapid increase in their numbers.

BIBLIOGRAPHY

Agassiz, Alexander.

1878. Development of *Lepidosteus*. Proceedings of American Academy of Arts and Science, Vol. 14, 65-76.

Evermann, B. W., and Clark, H. W.

1920. Lake Maxinkuckee. Department of Fish Conservation, State of Indiana, Publication 7, Vol. 1.

Forbes, S. A.

1878. The Food of Illinois Fishes. Bull. Illinois State Laboratory of Natural History, Vol. 1, 71-89.

1878. The Food of Fishes. Bull. Illinois State Laboratory of Natural History, Vol. 1, 18-65.

1888. Food Relations of Fresh Water Fishes: a Summary and Discussion. Bull. Illinois State Laboratory of Natural History, Vol. 2, 475-538.

1888. Studies of the Fresh Water Fishes. Bull. Illinois State Laboratory of Natural History, Vol. 2, 433-473.

1888. Food of the Fishes of the Mississippi Valley. Trans. American Fisheries Society, Vol. 17, 37-59.

1909. On the Distribution of the Fishes of Illinois. Bull. Illinois State Laboratory of Natural History, Vol. 8, 381-437.

1914. Fresh Water Fishes and Their Ecology. Illinois State Laboratory of Natural History. Separate. Urbana, Illinois.

Forbes, S. A., and Richardson, R. E.

1907. Fishes of Illinois. Bull. Illinois State Laboratory of Natural History, Vol. 3.

Hankinson, T. L.

1910. Ecological Notes on the Fishes of Walnut Lake, Michigan. Trans. American Fisheries Society, Vol. 40.

Harmier, S. F., Heidman, W. A., Bridge, T. W., and Boulenger, C. A.

1910. Fishes, Ascidiars, Etc. The Cambridge Natural History, Vol. 3.

Pearse, A. S.

1916. Food of the Shore Fishes of Certain Wisconsin Lakes. Bull. U. S. Bureau of Fisheries, Vol. 35, 245-292.

1920. Distribution and Food of Fishes of Green Lake, Wisconsin, in Summer. Bull. U. S. Bureau of Fisheries, Vol. 37, 253-272.

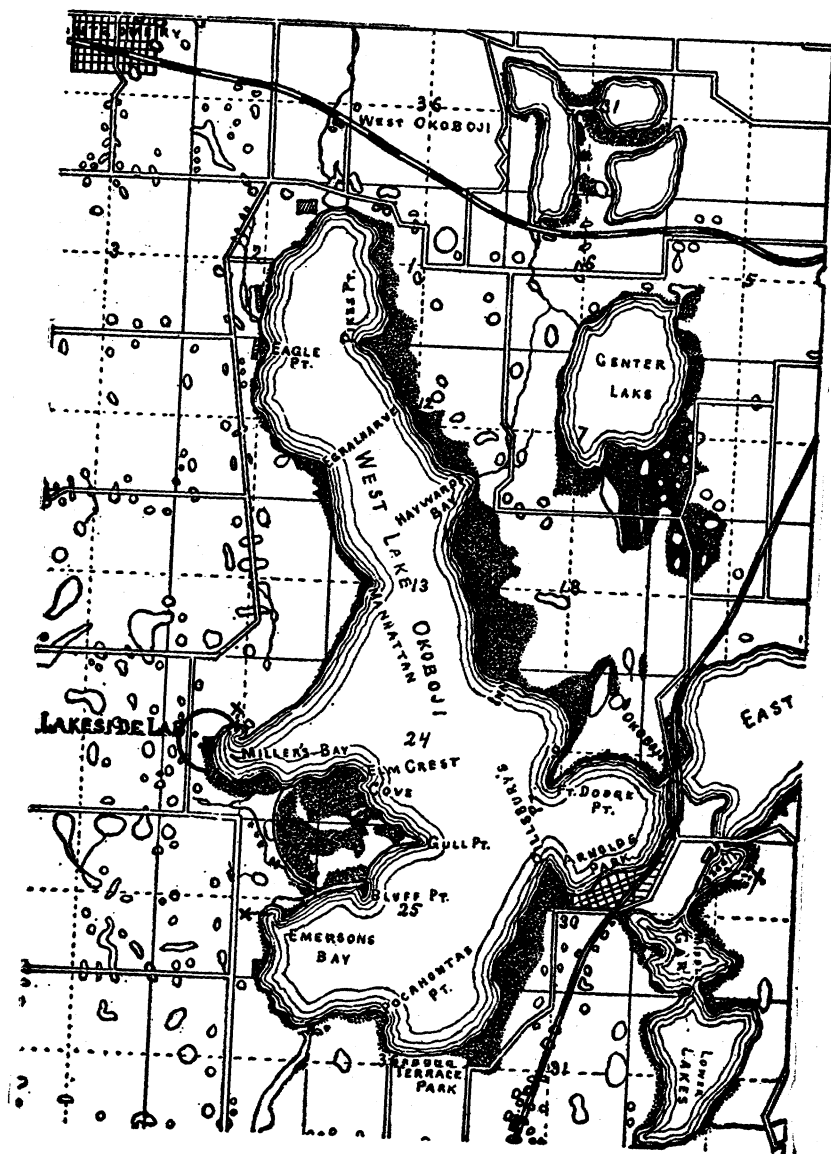
Richardson, R. E.

1911. Observations on Breeding Habits of Fishes at Havana, Illinois. Bull. Illinois State Laboratory of Natural History, Vol. 9, 405.

Wilder, B. G.

1877. Gar-pikes, Old and Young. Popular Science Monthly, Vol. 11, 1-12.

This is a detailed map of the West Okoboji area, showing West Lake, Center Lake, and various bays and points. The map includes a grid system with numbers 1-36 and letters A-J. Key locations labeled include Eagle Pt., Miller's Bay, Emersons Bay, and various parks like Terrace Park and Cedar Point. The map also shows the surrounding area, including Lakeside and East.



WATER MITES OF THE OKOBOJI REGION

RUTH MARSHALL

Rockford College

During the summer of 1924 the author spent some weeks at the Lakeside Laboratory of the University of Iowa, near Milford, in the Okoboji lake region of the northwestern part of the state. Through the courtesy of Dr. Frank A. Stromsten, Director of the Laboratory, facilities for collecting and studying the water mites were provided; the author wishes to acknowledge here the assistance which was received in the work. This paper is a contribution to the work of the Laboratory in securing data on the life of the lakes.

The Okoboji region is especially favorable for collecting hydra-carina, since it abounds in shallow lakes, ponds and sloughs which support an abundant aquatic vegetation. The conditions are typical of a recently glaciated region of the upper Mississippi basin. Collections were made in July and August. Most of the material was secured from West Okoboji, the largest of the lakes, and especially in and near Miller's Bay, where the Laboratory is located. Other lakes visited which yielded material were East Okoboji, Upper Gar, Spirit, Hottes, Little Spirit, Center, Robinson, and Sunken Lakes, Milford Creek at the dam, the canals and several of the sloughs in the region, and Loon Lake just over the Minnesota boundary line. A little material was secured in Clear Lake and in small pools near Charles City, some distance east of the Okoboji lakes. No mites were found in Welch, Drummond, Middle and Lower Gar lakes, nor in several of the muddy bordered sloughs visited.

In addition to the material secured by the author by the use of a modified Birge collecting net, several hundred parasitic mites of the genus *Unionicola* were added to the collection through the courtesy of Dr. H. M. Kelly, of Cornell College, who found them in the course of his investigations on the trematode parasites of the fresh water mussels of the lakes.

Altogether, several hundred individuals were secured; of these, the parasitic *Unionicolæ* and one species of *Piona* (*P. reighardi*),

claimed the largest number. Fifteen genera were represented and thirty-seven species and varieties, of which eight were *Arrhenuri*. Five of the species appear to be new and are here figured and described. In this connection it must be pointed out that many of the ninety or more recognized genera of the hydracarinae have never been thoroughly studied in this country, and there are as yet no published lists of the North American species of many of the genera. Consequently, the new species published here for the first time are, quite probably, not rare nor peculiar to the Okoboji region but only now recorded. In support of this view, it may be mentioned that no new species were found for the genera *Arrhenurus* and *Piona*, large genera which have been studied intensively. It is not assumed, of course, that the list of the species given here is at all complete.

The order in which the genera are arranged is one of convenience only; the larger and better known genera are given first, while the representatives of the "red mites" are recorded last.

Genus *ARRHENURUS*

The *Arrhenuri*, the largest genus of the water mites are always abundantly represented in waters like those of the Okoboji group. They were found in all the lakes except Center. Eight species were found, with more than one hundred and sixty individuals, besides several unidentified females and nymphs. Of these individuals, over half belong to three species of the "long tailed" forms (Subgenus *Megaluracarus*), *A. marshalli* Pier., *A. manubriator* Mar., and *A. megalurus* Mar. *Arrhenurus americanus* Mar. was also well represented; this species, with *A. marshalli*, the two American species of the genus most commonly found, claimed also the largest numbers here. The rarer species were *A. laticaudatus* Mar. (four individuals), *A. lyriger* Mar. (five), both found in West Okoboji; *A. laticornis* Mar. (two) in Upper Gar, and *A. trifolius* Mar. (one) in a small pool at the State Fish Hatchery, near Spirit Lake.

Genus *PIONA*

This genus was the most widely distributed, as is to be expected in a region like Okoboji; several hundred individuals were found, as they were present in nearly every collection made. Five species were identified, by far the most abundant being *P. reighardi* (Wol.). This species, perhaps the most common American water

mite, was found, both sexes and nymphs, to the number of several hundred. They were especially abundant in Loon Lake, Upper Gar and in some of the sloughs; and almost the entire catch from Robinson Lake consisted of mites of this species. *Piona pugilis* (Wol.) was found in Upper Gar, seven individuals; *P. inconstans* (Wol.), in Miller's Bay; *P. spinulosa* (Wol.), in Spirit Lake and Clear Lake; *P. rotunda* (Kram.), in Upper Gar. The last three species were each represented by one individual only.

Genus LIMNESIA

Over one hundred individuals of this common genus were found in the collecting grounds. Four species were identified, by far the largest being *Limnesia histrionica* (Herm.); this common and widely distributed species was especially abundant in Upper Gar and Center Lakes. The closely related form, *L. wolcotti* Piers., a variety of *L. histrionica*, was likewise found in several places. *Limnesia americana* Piers. was found (one female) in Clear Lake; and *L. paucispina* Wol. in Miller's Bay.

Genus UNIONICOLA

The genus is represented by four species, three being parasites in clams. The free form is the cosmopolitan species, *Unionicola crassipes* (Müll.); this was found only in Miller's Bay, but nearly fifty individuals were secured, most of them in the deeper water outside of the bar.

The parasitic species were found by Dr. H. M. Kelly, who kindly made the identifications of the fresh water mussels in which they occurred. *Unionicola abnormipes* (Wol.) was found to the number of several hundred in the examination of some three hundred clams, *Lampsilis luteolus*, collected in West Okoboji and Spirit Lakes, at several stations. *Unionicola ypsilophora* var. *haldermani* (Piers.), with several hundred individuals in all, was found in about fifty *Anodonta grandis* from Spirit Lake; and *U. intermedia* var. *wolcottii* (Piers.), about twenty-five individuals, was found in one clam (probably *Lampsilis luteolus*), taken in the Little Sioux River by Mr. Brenkleman. The infection of these clams by the mites was almost one hundred per cent; the largest number found in one individual was one hundred and eighty-six.

Genus LEBERTIA

The Okoboji region is not favorable for mites of this large genus which are more abundant in deeper and cooler waters. But

two individuals were found; these proved to be *Lebertia porosa* Thor, a cosmopolitan species. They were collected in Miller's Bay, outside of the bar.

Genus FRONTIPODA

One individual of the common species, *Frontipoda americana* Mar., was found in Loon Lake, Minnesota.

Genus OXUS

Oxus intermedius new species

Plate I, figs. 1-3

Three mites of this genus were found in a brief dredging in the border of Loon Lake, a shallow pond near Spirit Lake. They appear to belong to a new species.

The margins of the epimeral shield come barely into view on the dorsal surface; the posterior border has a deep U-shaped bay in which lies the genital area. The genital plates do not project beyond the bay, however, as is usual in *Oxus*. It is assumed, because of the deep set position of the genital plates, that the specimens are males. These plates are elongated and bear several very fine hairs each; the three acetabula usually found here could not be made out. The surface of the epimeral shield is closely beset with very fine points; the anterior part is pinkish in color, the rest of it greenish. The dorsal side of the body shows dark blotches. The palpi are rather small; the legs are greenish blue, the fourth ending in the usual long saber-like point instead of claws. The largest of the three individuals found measured 1.1 mm. in length and 0.6 mm. in the widest part; the two smaller were 0.9 mm. long and 0.6 mm. wide. In the latter, presumably somewhat younger individuals, the ventral shield was relatively a little larger than in the largest individual, from which the drawings were made.

Genus NEUMANIA

Pl. II, figs. 10-12

Six species of the genus are here represented, one of which is new. *Neumania tenuipalpis* Mar. was the most abundant, being found in West and East Okoboji, Upper Gar and Loon Lakes and at the dam in Milford Creek. Three of the eighteen individuals found were females. As this sex has not been known before, a figure of the genital area is given (fig. 10). The living animals of both sexes show two wedge-shaped areas on the dorsal side which have very dark brown dots on a yellowish background, while a pale yellowish blotch lies anterior to them. The eyes are red. The body is covered with fine lines.

The new species, to which the name *N. okobojica* has been given,

represented by one female individual only, was found in Upper Gar Lake.

Neumania okobojica new species

It is a large mite, 1.45 mm. long and 1.2 mm. wide, oval, dull greenish in color, with blue plates and legs and a heavy integument. The epimera are of the usual form and size, but the underlying braces from the first pair cannot be made out in a surface view. The palpi are very small but stout. The genital area of the female is close to the epimera and is very distinctive, since the plates of either side bearing the acetabula are separated, as shown in the figure (fig. 11).

The other species of the genus which were found were *N. punctata* Mar. (at the Narrows and in the "Little Canal"), three males; *N. ovata* Mar. (one, "Little Canal"), *N. semicircularis* Mar. (one each in Miller's Bay and Emerson Bay); *N. brevibranchiata* Mar. (two males, in Upper Gar).

Genus HYGROBATES

The genus is characteristically a northern one; it is reported as common in northern Europe, and one species has been found by the author in large numbers in Alaska. But one individual was found in the Okoboji collections; this was a newly emerged male found in Miller's Bay outside of the bar. It appears to represent a new species, not hitherto described but already studied by the author.

Hygrobates ruber new species

Plate I, figs. 5-7

The new species is seen to resemble *H. calliger* Piers, differing from the European form in several details, especially in the genital plates. The figure given of the ventral plates of a mature female (fig. 5) was drawn from material collected by Professor F. C. Baker in Lake Winnebago, Wisconsin, and kindly turned over to the author. The epimeral plates are not large; they lie close together and the genital area is not far removed from them. The palpi are of the characteristic size and shape, with a well developed spiny peg on the second joint. The body in both sexes measures about 0.9 mm. The dorsal side of the body is brownish with a red streak on it; this latter character has suggested the specific name, *H. ruber*.

Genus KOENIKEA

This genus is represented here by the fairly common species, *Koenikea concava* Wol., the only species so far recorded for this continent. Eight individuals were found, taken from Miller's Bay, Upper Gar, the Narrows and Center Lake.

Genus *XYSTONATUS*

Of *Xystonatus asper* Wol., one individual was found in each of Upper Hottes and Clear Lakes. It is the only species of the genus recorded for North America.

Genus *HYDRYPHANTES*

Adults and nymphs to the number of eighteen, found in four of the lakes (Hottes, Robinson, Sunken and Spirit), furnish the material for the formation of a new species of this genus.

Hydryphantes tenuabilis new species

Plate II, fig. 9; Plate III, figs. 16-18

The dorsal plate bearing the median eye is here reduced to an anterior bar with two divergent limbs, the posterior divided ends of which are somewhat variable in shape, as reported also in other species, and only faintly outlined. In the form of this plate, a character important in distinguishing the species of the genus, the new species resembles *H. ramosus* described by Daday from Paraguay. The body is ovate, bright deep red in color, and the largest specimen is 1.05 mm. long. The surface is thickly beset with fine rounded elevations. The ventral plates are close together, a little farther removed in younger individuals; all bear short bristles or hairs. The genital area is large, in the center of the body; each lateral plate bears three acetabula of about equal size. The genital plates of the nymph have two acetabula each. The legs are short, and the last three bear swimming hairs.

Genus *DIPLODONTUS*

One species of this large genus was found; it is a common species, although here described for the first time, and given a name, *D. americanus*. In the Okoboji region it was found in Upper Gar, at the Narrows, and in Spirit, Sunken and Loon Lakes, twenty-eight individuals being secured. Of these, several were nymphs, and a few were newly emerged adults, all taken in late July and early August. The bodies of the females were filled with large globular eggs.

Diplodontus americanus new species

Pl. I, fig. 4; Pl. II, fig. 8; Pl. III, figs. 13-15

The body is almost circular in outline, orange red, with a large dark scalloped area on the dorsal side, the same coloring as in *D. despicens* (Müll.), a very common and widely distributed species in the Old World and reported also for the Americas. Although the two species are otherwise very similar, *D. americanus* has a different form of genital plates, and these are closer in toward the last epimera and also broader posteriorly. In these particulars it more closely resembles *D. peregrinus* Koen., found in Brazil. In the palps,

the projection of the fourth joint is a little smaller than the fifth joint with which it forms the claw. The epimeral plates are typical of the genus and bear many hairs. All of the ventral plates are close together in the very young adults. In the nymph, the genital area has four large acetabula. Newly emerged individuals measure 0.75 mm. in length; old adults were found from 1.3 to 1.75 mm. In other collections by the author they have been found as large as two millimeters.

Genus EYLAIIS

Only one individual of this large genus of the "red mites" was secured. This was found at the dam, Milford Creek. Its identification is uncertain; it does not seem to conform to any of the few species of the genus as yet described for North America. Since determination of the species depends largely on details of the small dorsal eye plate, a character known to have considerable range of variation, it does not seem wise to record a species from the examination of only one specimen.

Genus HYDRACHNA

It is surprising to find that this large and common genus was not represented in the collections from the Okoboji waters. One individual, a young one, was found in Clear Lake, but it was not identified. Doubtless more systematic collecting at other stations would have yielded more material.

Corrections

In the paper, "Water mites of Alaska and the Canadian Northwest" (Trans. A.M.S., XLIII, 4, 1924), two regrettable errors occur, to which the attention of the author has been called in private correspondence. The specific name, *octoporus* (p. 238), being preoccupied, that of the new species will be changed to *Hygrobates neoöctoporus*. The new species *longiseta* (p. 243) given to *Piona* should be *Neumania longiseta*.

LIST OF THE SPECIES

1. *Eylais* sp.
2. *Hydryphantes tenuabilis* new species
3. *Diplodontus americanus* new species
4. *Hydrachna* sp.
5. *Limnesia histrionica* (Herm.)
6. *Limnesia histrionica* var. *wolcottii* Piers.
7. *Limnesia americana* Piers.
8. *Limnesia paucispina* Wol.

9. *Lebertia porosa* Thor.
10. *Frontipoda americana* Mar.
11. *Oxus intermedius* new species
12. *Hygrobates ruber* new species
13. *Unionicola crassipes* (Müll.)
14. *Unionicola abnormipes* (Wol.)
15. *Unionicola ypsilophora* var. *haldermani* (Piers.)
16. *Unionicola intermedia* var. *wolcottii* (Piers.)
17. *Neumania tenuipalpis* Mar.
18. *Neumania punctata* Mar.
19. *Neumania ovata* Mar.
20. *Neumania semicircularis* Mar.
21. *Neumania brevibranchiata* Mar.
22. *Neumania okobojica* new species
23. *Koenikea concava* Wol.
24. *Piona reighardi* (Wol.)
25. *Piona pugilis* (Wol.)
26. *Piona inconstans* (Wol.)
27. *Piona spinulosa* (Wol.)
28. *Piona rotunda* (Kram.)
29. *Xystonatus asper* Wol.
30. *Arrhenurus marshalli* Piers.
31. *Arrhenurus megalurus* Mar.
32. *Arrhenurus manubriator* Mar.
33. *Arrhenurus laticaudatus* Mar.
34. *Arrhenurus laticornis* Mar.
35. *Arrhenurus lyriger* Mar.
36. *Arrhenurus trifolius* Mar.
37. *Arrhenurus americanus* Mar.

PLATES

PLATE I

- Fig. 1. *Oxus intermedius*, dorsal view
- Fig. 2. *Oxus intermedius*, lateral view
- Fig. 3. *Oxus intermedius*, ventral view
- Fig. 4. *Diplodontus americanus*, genital area of the nymph
- Fig. 5. *Hygrobates ruber*, ventral plates of the female
- Fig. 6. *Hygrobates ruber*, genital area of the male
- Fig. 7. *Hygrobates ruber*, right palpus

PLATE I

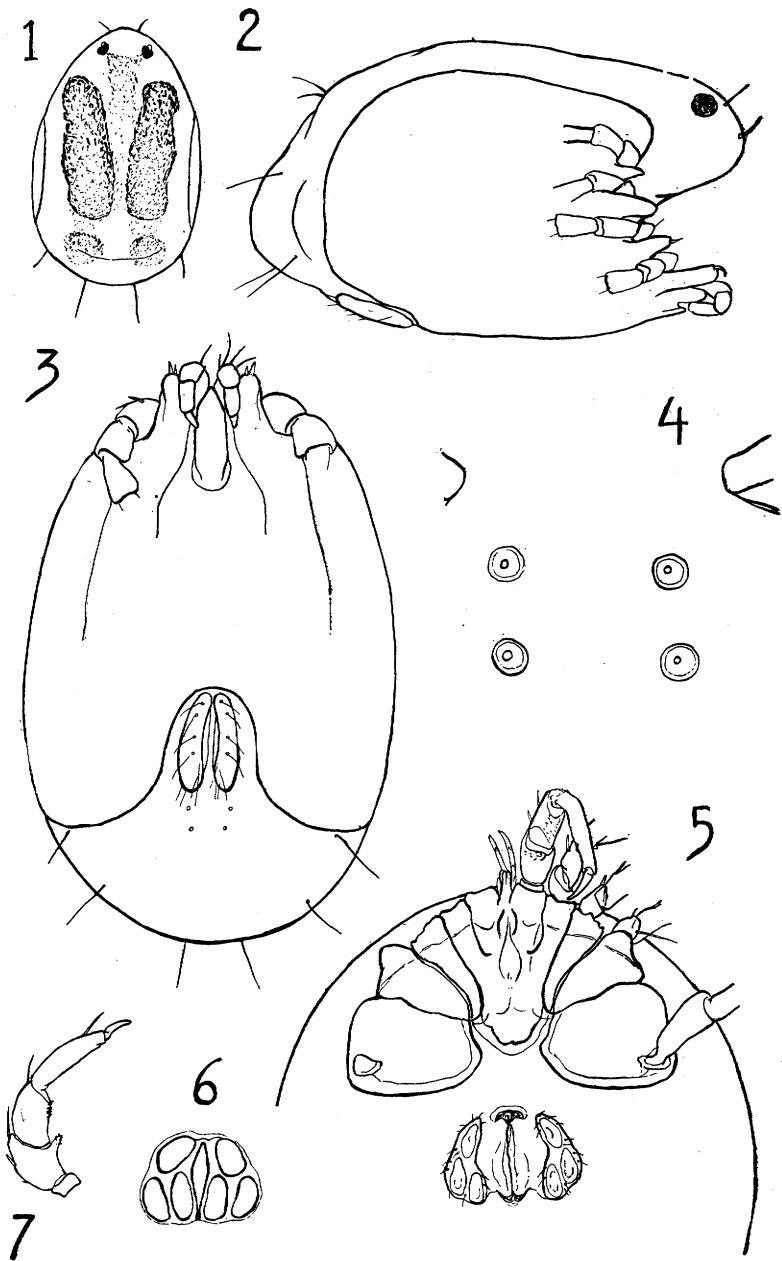


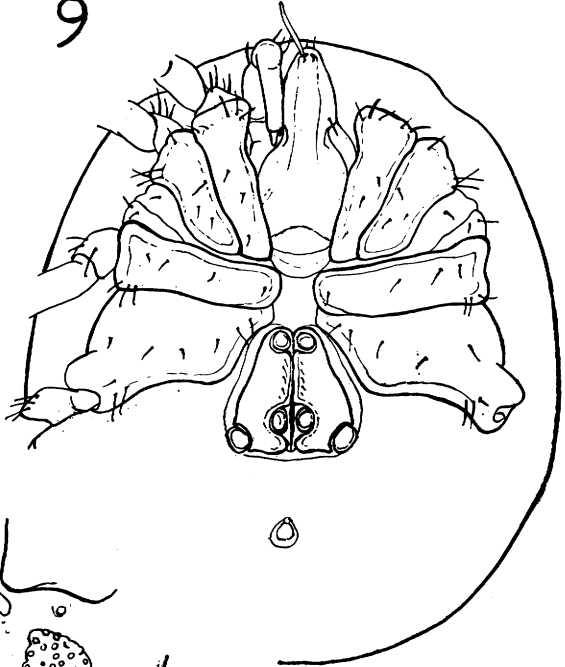
PLATE II

- Fig. 8. *Diplodontus americanus*, the two eyes of the left side
Fig. 9. *Hydryphantes tenuabilis*, ventral view
Fig. 10. *Neumania tenuipalpis*, genital area of the female
Fig. 11. *Neumania okobojica*, ventral plates of the female
Fig. 12. *Neumania okobojica*, palpus

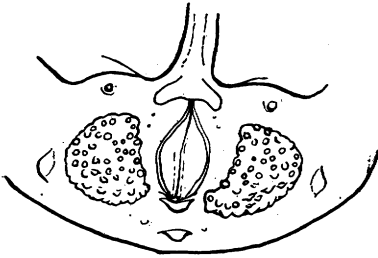
8



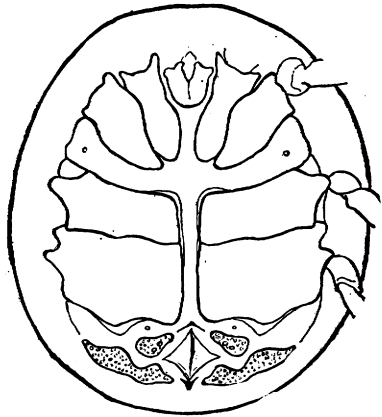
9



10



11



12

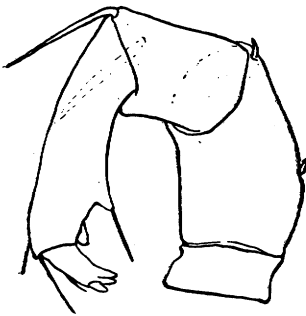
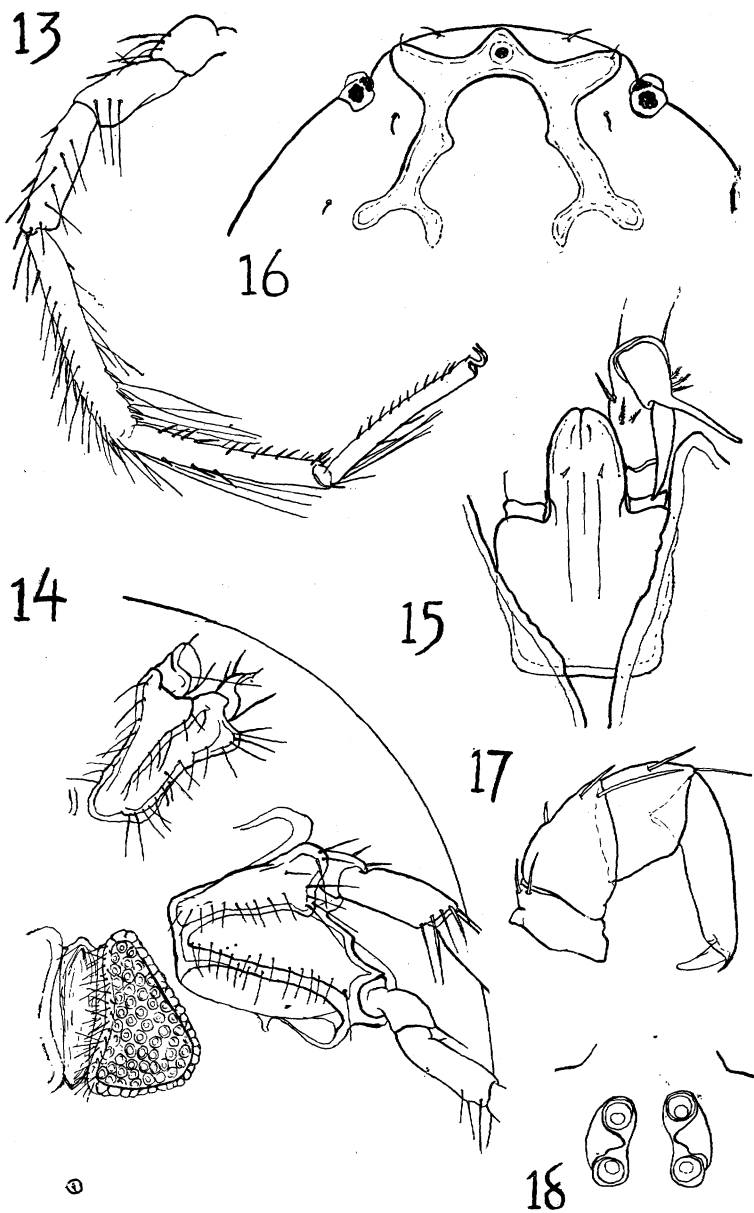


PLATE III

- Fig. 13. *Diplodontus americanus*, fourth leg
- Fig. 14. *Diplodontus americanus*, ventral plates, left side
- Fig. 15. *Diplodontus americanus*, capitulum and left palpus
- Fig. 16. *Hydryphantes tenuabilis*, eye plate
- Fig. 17. *Hydryphantes tenuabilis*, palpus
- Fig. 18. *Hydryphantes tenuabilis*, genital area of the nymph

PLATE III



UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

VOLUME XI

NUMBER 10

PAPERS ON IOWA FUNGI

PUBLISHED BY THE UNIVERSITY, IOWA CITY, IOWA

Each.
U. S. Iowa Library
5-21-1934 ✓

CONTENTS

The Iowa Species of Russula

GRACE WINTERS

Occurrence of Mycorrhiza in Iowa Forest Plants

M. L. LOHMAN

THE IOWA SPECIES OF RUSSULA

GRACE WINTERS

INTRODUCTION

The name *Russula* was first used by Persoon in 1796 to designate a section of the genus *Agaricus*. In his Synopsis of 1801 (5) he includes twenty-four species in the section. *R. emetica*, described by Schaeffer in 1774 as *Agaricus emeticus*, is usually regarded as the type. Among European botanists Persoon, Schaeffer, Fries, Quelet, and Romell have studied the genus extensively. In America most of the work on *Russula* has been contributed by Peck, Kauffman, (3) Beardslee, (1) and Burlingham (2).

Practically no work has been done on the local occurrence of the genus in Iowa, and in view of this fact a taxonomic study of Russulas was begun in the summer of 1924. The work has been carried on in the mycological laboratory of the State University of Iowa, under the direction of Professor G. W. Martin. The mycological herbarium contains thirty-nine determined species of *Russula* collected within the state. The only previous mention of Russulas in Iowa seems to be the three reported by Shimek (6) from the Lake Okoboji region. The thirty-nine species at Iowa City include specimens from Johnson, Dubuque, and Clayton counties, which were gathered over a period of three years from 1923 to 1926.

In this state, Russulas form a conspicuous part of the mycological undergrowth in open oak woods. Usually they make their appearance in the middle of the summer and last through early fall.

The present study is only a beginning, as much work remains to be done on this genus. It is hoped that in the future collections can be secured from various parts of the state which will permit a more comprehensive knowledge of the Russulas of Iowa. In compiling the descriptions of species constant reference has been made to the works of Beardslee, Burlingham, and Kauffman, especially the last-named. The order of species is, in general, that of Kauffman.

TECHNIQUE

For collecting Russulas no elaborate equipment is necessary; a large market-basket and plenty of newspaper are all that is needed.

A heavy knife or narrow trowel is handy to loosen the soil around the base of the stipe, for while no volva is present, the complete stipe should always be secured.

Each individual collection can readily be kept separate by wrapping in newspaper and packing loosely in a basket. This procedure is important, since many of the species are much alike and without a great deal of experience it is difficult to distinguish between them. The spores are not as liable to become mixed when each collection is kept separate, and any spore-prints deposited on a wrapper will be with the specimens that produced them.

In the study of *Russulas* it is essential to secure a good spore-print. Only mature pilei should be used. Cut the stipe near the pileus and place the pileus with gills down on a white paper. Cover with a beaker or bell-jar and leave for several hours. Black paper may be used where the gills look white. With mature specimens a mass of spores will be deposited whose color is distinct. Often small worms or insects are bothersome. If so, a few crystals of paradichlorobenzene under the bell-jar will kill the pests without injuring the specimens.

The value of adequate collection data can not be over-stressed. They should include date, locality, habitat, color of spore-print, taste, odor, and name of collector. These data can be effectively listed on the slip on which the spore-print is deposited. As the specimen is unwrapped, in preparation for the work in the laboratory, a small piece of the pileus may be tasted. It is not at all difficult to distinguish between the mild and acrid forms, as the difference is quite pronounced.

The taste is an extremely important taxonomic character and must be obtained when the specimen is fresh. There are several forms in the *Russula* collection at Iowa City where the spore-print is lacking and the taste not recorded, hence it has been impossible to identify them with certainty.

A record of the locality in which collections are made is important, especially when one is working over a given area such as a state. Material may be abundant in one part of the area and scanty in another. Some species of *Russula* are found only in open oak woods, others among conifers. In this state *Russulas* have been collected only in open oak woods. A description or mention of habitat often aids in identification.

The summer of 1924 was hot and rainy, an ideal season for fungi.

Russulas are summer and early fall forms, August being ordinarily the best month for their collection. Though the latter part of the summer of 1925 was dry, the early fall was rainy, which resulted in an excellent production of Russulas in many forms. Abundant collections were made until the middle of October, which is rather unusual for this region.

Drying of the specimens is simple. When the sun is bright enough and the atmosphere not too humid, air drying is effective. If this method can not be used, the specimens may be dried in a slightly heated oven. In the laboratory at Iowa City the specimens are placed on a wire net over a radiator and dried. In this process the heat kills the parasites. After the specimens are thoroughly dry, they are ready to be put in the herbarium, the spore-print and collection data being filed with each specimen. It is well to add a small amount of naphthalene to guard against further attack by insects.

In identification work, microscopic cross-sections of the gills are often of service. A small piece of pileus with gills attached may be placed between pieces of pith and sectioned with a razor. These sections must be sufficiently thin for the study of the structure of the hymenium and trama. Dried specimens lend themselves very nicely to sectioning. A small portion of the pileus may be soaked in water for a short time, then sectioned in the same manner as the fresh material. When the section is placed on the slide a drop of 7 per cent potassium hydroxide may be added. This causes the cells to distend, giving them a more natural appearance. An ordinary compound microscope with low and high power objectives may be employed to examine the slide. The low power gives the general contour of the section, while the higher power serves to show the details of the hymenium. An oil immersion objective is not necessary in the study of cross-sections, but is very helpful in studying the spores. It is often necessary to resort to the use of microscopic sections when identifying closely related species.

DISCUSSION OF THE GENUS

The genus *Russula* may be characterized as follows: Trama vesiculose, without milky juice; pileus fleshy, continuous with stipe, variable in color, with or without separable pellicle, dry or viscid; margin even or striate; gills attached, rigid but fragile; stem central, rigid; veil absent, spores white, creamy, or yellow; taste acrid or mild; odor none or characteristic in a few species only.

Russula is a very distinct genus, most closely related to *Lactarius*, from which it differs by its lack of a milky juice. *Hygraphorus* differs in the thicker and more waxy nature of the gills, although there are evident signs of relationship between this genus and certain species of *Russula*.

The most distinctive feature of the genus is the character of the trama, which with that of the *Lactarii* is most unique among the Agaricaceæ. Hyphæ of the usual slender, filamentous type, as found in the other genera, are rather scanty and interweave among clusters of thin-walled, parenchyma-like, isodiametric cells, forming the so-called vesiculose trama; this accounts for the more or less brittle consistency of the pileus.

The hymenium and subhymenium are, in some species, quite characteristic. Cystidia may or may not be present; if present, they may be few, scattered, abundant, short, blunt, clavate or long and pointed. This character is found to be constant for each species. The subhymenium may be distinct or may merge gradually into the tissue of the trama.

While the trama is the most outstanding generic character, spore-prints and spores are the most essential means of settling the identity of closely related species. The color of the spore-print is constant for each species, but may fade with age, hence all herbarium spore-prints should be accompanied by careful notes of the print when fresh. The color varies from a pure chalk-white to a rather pronounced ochre and is one of the most valuable diagnostic characters.

By staining the spores with Melzer's¹ reagent and using an oil immersion objective, the spore-markings may be determined. This reagent stains the markings on the spore wall without staining the wall itself. If this reagent is not used, the markings may be made out only by means of an oil immersion objective and even then with difficulty and uncertainty.

The spores may be divided into two groups, according to the markings; the reticulate and echinulate types. The echinulate group is further subdivided into those with long spines and those with blunt spines; the reticulate group also consists of two types, those with crests or ridges and those with fine connections. When the diagnos-

¹ Melzer's reagent (4)

Potassium Iodide

1.5 grams

Iodine

.5 grams

Water

20.0 grams

Add to this solution an equal amount of chloral hydrate.

tie characters are almost identical, the spore markings may be the determining factor. In fact, in closely related species, the presence or absence of cystidia and the spore markings are the only differentiating factors.

The pileus may be convex, plane, or depressed in the center, and exhibits a great variety of colors: red, purple, yellow, green, and white. The specimens of the same collection may vary in color, according to light exposure or age.

A differentiated pellicle composed of more or less specialized hyphae is present on the surface of the pileus. It may become viscid in wet weather, or may remain dry and become pruinose or velvety. The pellicle is somewhat separable along the margin and in some species may be easily peeled from nearly the whole surface.

The flesh of the pileus, when fresh, is white or whitish, or it may be tinged grayish or purplish. In many of the red forms, the flesh under the pellicle is tinged red or reddish; on exposure to the air, after bruising or in age, it may turn ochraceous or blackish.

The margin may be even or striate, or even at first, becoming striate in age. In species with thin pilei, the lines of attachment of the gills to the pileus show through as raised ridges and these striations may extend toward the center of the pileus. In the species with firm thick pilei the striations are not as clearly marked or are obscurely developed on the margin. They may appear when the plant becomes old. This character is somewhat variable and must be used with caution.

The gills are brittle, thin, with acute edges, simple or forked, of equal or unequal length. The colors for the different species are of all shades between white and deep ochre-yellow. This fact alone separates them from any spore-color groups of the Agaricaceae. The gills may become darker with age or may stain where bruised. The shape and width are constant and are of value in identification.

The stem is central or nearly so; solid, firm, spongy or stuffed, becoming hollow, but never fibrous, usually white, sometimes red or slightly ochraceous, in some species changing to ashy or brownish where bruised.

The taste is sharply acrid in some species, slowly or slightly acrid in others, and entirely mild in a considerable number. This is an important character for the identification of the species and is fairly constant. In all species it is necessary to have fresh specimens in order to determine whether or not acidity is present. Almost all

the species are edible after careful cooking, since even the peppery forms then lose their sharp taste; in any case the mild species are said to be perfectly safe when fresh, young, and clean.

The odor of some species is quite characteristic and should always be considered. One must not confuse this test by applying it to plants already in the first stages of decay.

KEY TO THE IOWA SPECIES OF RUSSULA

Pileus some shade of red or purple.....	1
Pileus not some shade of red or purple.....	27
1- Spores pure white in mass—not creamy white.....	2
1- Spores not white in mass including creamy white.....	10
2- Taste promptly acrid.....	3
2- Taste mild or tardily acrid.....	6
3- Flesh white under pellicle.....	4
3- Flesh red under pellicle.....	5
4- Gills thin, crowded, moderately broad; margin striate; very fragile.....	<i>R. fragilis</i>
4- Gills subdistant, attached by a point; edge even.....	<i>R. fallax</i>
5- Pileus rosy to blood red, color even; pellicle separable; margin strongly tuberculate striate.....	<i>R. emetica</i>
5- Pileus darker, often purplish; pellicle adnate, scarcely separable; often yellow spotted; margin slightly striatulate in age.....	<i>R. atropurpurea</i>
6- Edge of gills flocculose-crenulate; blood-red; viscid, when dry as if with bloom; striate only when fully expanded.....	<i>R. purpurina</i>
6- Not as above.....	7
7- Pileus purplish or deep rose pink, later variegated with olive or greenish; flesh grayish, under pellicle; often tardily acrid.....	<i>R. variata</i>
7- Not as above.....	8
8- Pileus rigid, unpolished; margin obtuse; not striate; sometimes slightly bitterish or subacrid.....	<i>R. lepida</i>
8- Pileus thin; fragile.....	9
9- Pileus 2-5 cm. broad; pink or bright flesh, unicolorous.....	<i>R. uncialis</i>
9- Pileus 5-14 cm. broad; bright rosy red, shading into yellowish blotches.....	<i>R. subdepallens</i>
10- Taste acrid.....	11
10- Taste mild.....	15
11- Taste tardily but truly acrid.....	12
11- Taste promptly acrid.....	14
12- Pileus 6-12 cm. broad; uniform red or spotted; gills crowded, narrow, fragile, white to yellow ochraceous.....	<i>R. tenuiceps</i>
12- Not as above.....	13
13- Pileus rosy red; 3-6 cm. broad; spores and gills creamy white.....	<i>R. sanguinea</i>
13- Pileus Corinthian red, fading; up to 9 cm. broad; spores ochraceous in mass; gills yellowish.....	<i>R. corinthiirubra</i>
14- Pileus 2-5 cm. broad; pale dull red to rosy red; soon dry; stem white or rosy tinged.....	<i>R. subpunctata</i>
14- Pileus 5-7 cm. broad; deep rosy red; viscid when moist; stem white, never red.....	<i>R. veterinosa</i>
15- Flesh white, unchanging.....	16
15- Flesh changing with age or where wounded, or tinged under pellicle.....	22
16- Pileus salmon or salmon tinged to dull red in center; margin drooping; spores maize yellow.....	<i>R. humidicola</i>
16- Pileus without salmon color or tinge; spores not maize yellow.....	17
17- Pileus 2.5-8 cm. broad; red to paler, yellowish on disk; margin even, slightly striate when old; stem white to yellowish at base.....	<i>R. luteobasis</i>

17- Not as above.....	18
18- Pileus 2-5 cm. broad; some shade of red or purple, fading to yellowish on disk; stem 2-5 cm. long, 4-6 mm. thick, slender, white.....	<i>R. chamaeleontina</i>
18- Not as above.....	19
19- Pileus 2.5-5 cm. broad; rosy red to flesh red fading to yellowish on disk, stem white or rose tinged, 2.5-5 cm. long, 5-12 mm. thick, tapering upwards.....	<i>R. roseipes</i>
19- Not as above.....	20
20- Pileus rosy-flesh to peach color; fragile; gills white at first to bright ochraceous yellow.....	<i>R. amygdaloides</i>
20- Not as above.....	21
21- Pileus 8-12 cm. broad; dull colors, reddish purple, sordid red, reddish predominating; gills ochraceous becoming darker with age.....	<i>R. alutacea</i>
21- Pileus 5-10 cm. broad; color from buff to reddish-brown to dark dull red, fading; gills white to cream or buff.....	<i>R. integra</i>
22- Flesh staining slowly red then black where wounded.....	<i>R. rubescens</i>
22- Not staining slowly red then black where wounded.....	23
23- Flesh red under cuticle; firm; blood red.....	<i>R. borealis</i>
23- Flesh not red.....	24
24- Odor disagreeable in age; pileus purplish red, olivaceous, variegated; stem changing to ochraceous brown where handled.....	<i>R. xerampelina</i>
24- Odor none; pileus not variegated with olive tints.....	25
25- Purple or dark purplish red; cuticle adnate; gills yellowish to bright ochraceous buff.....	<i>R. ochrophylla</i>
25- Not as above.....	26
26- Pileus 4-7 cm. broad; rather pliant; dark dull red, sometimes blackish on disk; stem becoming ashy or blackish.....	<i>R. obscura</i>
26- Pileus 5-12 cm. broad; firm; orange-red to ochre on disk, darker red on margin; stem becoming cinereous.....	<i>R. decolorans</i>
27- Spores white in mass, not creamy white.....	28
27- Spores not white in mass, including creamy white.....	39
28- Pileus white.....	29
28- Pileus not white.....	31
29- Pileus 8-15 cm. broad; gills short and long alternating; mild to weakly acid.....	<i>R. delicata</i>
29- Pileus 2.5-5 cm. broad; gills not short and long alternating; acid.....	30
30- Margin even.....	<i>R. albidula</i>
30- Margin striate.....	<i>R. fragilis</i>
31- Flesh white, unchanging, not tinged under cuticle.....	32
31- Flesh white, changing or tinged under cuticle.....	37
32- Stem stained at base by cinnabar red stains.....	<i>R. foetentula</i>
32- Base not stained at base by cinnabar red stains.....	33
33- Taste tardily and slightly bitterish.....	34
33- Taste mild.....	35
34- Pileus 6-12 cm. broad; soon dry; stem 4-5 cm. long.....	<i>R. ochroleucoides</i>
34- Pileus 3-6 cm. broad; viscid; stem 3-4 cm. long.....	<i>R. raoultii</i>
35- Pileus 5-10 cm. broad; pale grayish green paler or sub-ochraceous in center; margin even; spores white tinged yellow.....	<i>R. viridella</i>
35- Not as above.....	36
36- Margin striate when mature; cystidia present; pileus with crust-like areas; viscid when young or moist.....	<i>R. crustosa</i>
36- Margin not striate; no cystidia; pileus with floccose pulverulent areas; dry.....	<i>R. virescens</i>
37- Pileus whitish, clouded with umber; flesh changing to reddish where bruised then blackish.....	<i>R. nigricans</i>
37- Not as above.....	38
38- Pileus 3-7 cm. broad; straw color to brown; striate.....	<i>R. pectinatoides</i>
38- Pileus 5-12 cm. broad; variegated; not striate.....	<i>R. variata</i>
39- Flesh white, not changing, tinged under pellicle.....	40
39- Flesh changing with age or tinged under pellicle.....	41

- 40- Pileus purple-brown on disk; margin dull garnet; mild to somewhat nauseous *R. nauseosa*
 40- Not as above..... 42
 41- Pileus buff to reddish brown to dull red; spore-print cream yellow to pale ochraceous..... *R. integra*
 41- Pileus umber-yellow to golden yellow; spore-print maize yellow..... *R. flaviceps*
 42- Flesh thick on disk, thin elsewhere; grayish or grayish purple under pellicle; odor unpleasant when fresh..... *R. xerampelina*
 42- Flesh not grayish nor grayish purple under pellicle..... 43
 43- Pileus 3-7 cm. broad; from dingy straw color through to umber brown; margin striate..... *R. pectinatoides*
 43- Pileus 5-8 cm. broad; dull yellow; even or slightly striate in age..... *R. flava*

DESCRIPTION OF SPECIES

1. *Russula delica* Fr.

Pileus 8-15 cm. broad, firm, convex—umbilicate then depressed to infundibuliform, *dull white*, sometimes with rusty-brown stains, *unpolished*, glabrous, pubescent or obscurely tomentose, even, dry, margin at first involute, not striate.

Flesh compact, white or whitish, not changing where bruised.

Gills subdecurrent, narrowed behind, broader in middle, distant or subdistant, thickish, short and long alternating, few forked, *white or whitish*, edge often distinctly greenish.

Stem 2-5 cm. long, 1.5-2 cm. thick, *short*, stout, *solid*, equal or subequal or tapering down, white becoming dingy, not turning blackish when bruised, glabrous or subtomentose above, often with a narrow pale-green zone at apex.

Taste mild to tardily but weakly acrid.

Odor none.

Spores globose, 9-10 microns, tuberculate, white in mass. This species is reported by Shimek from the Okoboji region. I have not collected it.

2. *Russula nigricans* Fr.

Pileus 7-15 cm. broad, subrigid, convex then depressed to subinfundibuliform; margin at first incurved then spreading and elevated, often irregularly wavy, at first whitish and clouded with umber, *soon smoky-umber*, subviscid at first, glabrous, even on margin.

Flesh, compact, white, *changing to reddish* where bruised, *then blackish*.

Gills narrowed or rounded behind, adnexed, thick and firm, *subdistant to distant*, short and long alternating, white becoming grayish, reddish at first when bruised.

Stem 2-6 cm. long, 1-3 cm. thick, *solid*, hard, stout, white at first, at length *smoky-umber*, *reddish then blackish where bruised*.

Taste mild, sometimes tardily but slightly acrid.

Odor none.

Spores subglobose, 8-10 microns, reticulate, white in mass.

Cystidia short and blunt.

3. *Russula virescens* Fr.

Pileus 5-12 cm. broad, at first globose, soon convex and expanded, often somewhat depressed, firm, *dry* or velvety, surface of disk broken into many floccose or pulverulent areas or patches, green or grayish green, the margin not striate or rarely so, cuticle scarcely distinguishable or separable.

Flesh white.

Gills white, rather close, narrowed towards stem, almost or entirely free, few shorter and forked.

Stem 3-7 cm. long, 1-2 cm. thick, white, firm, equal or subequal, solid or spongy.

Spores subglobose, 6-8 microns, echinulate, with few very fine reticulations, spines scattered and blunt, white in mass.

Cystidia none, no differentiated subhymenium.

4. *Russula crustosa* Pk.

Pileus 5-12 cm. broad, firm, convex then expanded and depressed in the center, surface cracked except on disk, the *areas crustlike*, sordid cream-color, dirty brownish or ochraceous, usually tinged with olive or green, viscid when young or moist, especially on the disk, *striate on margin* when mature.

Flesh white.

Gills dull white, dingy cream color in age, rather broad in front, narrowed toward stem, adnexed or free, *thick, distinct*, not crowded, rather brittle, few forked, few short.

Stem 3-6 cm. long, 1-2.5 cm. thick, short, stout, spongy-stuffed, subequal, ventricose or white.

Taste mild.

Odor none.

Spores broadly ovate, 7-8 x 8-10 microns, reticulate, white in mass.

Cystidia rather numerous extending through subhymenium.

5. *Russula viridella* Pk.

Pileus subglobose or very convex, becoming nearly plane or centrally depressed, 5-10 cm. broad, surface pale grayish-green, paler or subochraceous in the center, dry, soon minutely squamulose or furfuraceous, except in the center, margin even.

Flesh white.

Gills white, few short ones present, some forked, thin, narrow, close.

Stem white, equal or nearly so, even, solid or spongy within, 5-7.5 cm. long, 1-1.6 cm. thick.

Taste mild.

Odor none.

Spores subglobose, 7-8 microns in diameter, reticulations very fine, white tinged with yellow in mass.

Cystidia subfusiform 80 x 16 microns.

6. *Russula ochrroleucoides* Kauff.

Pileus 6-12 cm. broad, large, rigid, convex, soon expanded-plane, varying *straw yellow to pale ochraceous*, usually dull ochre to reddish ochre toward center, pellicle adnate, soon dry, pulverulent or subrimose, even on the obtuse margin.

Flesh, *thick*, compact, white, unchanging or slightly sordid in age.

Gills adnexed or free, rather narrow, rounded or slightly broader in front, *white* or whitish, close to subdistant, shorter ones intermingled, often forked in posterior part, intervenose.

Stem 4-6 cm. long, 1.5-2 cm. thick, short, rigid, equal or tapering slightly downward, white, glabrous or subpruinose, spongy-solid, even or obscurely wrinkled.

Taste tardily and slightly bitterish, acrid or disagreeably bitter.

Odor faintly aromatic or none.

Spores globose, 7-9 microns, reticulate, white in mass.

Cystidia few to moderately abundant.

7. *Russula raoultii* Quel.

Pileus broadly convex, then plane or slightly depressed in center; 3-6 cm. broad, surface straw-yellow or massicot yellow, viscid, glabrous, margin even or at length very faintly striate.

Flesh pure white, unchanging.

Gills white, some short ones intermingled, rarely forking next to the stipe, interspaces slightly venose, narrow, 2-6 mm. broad, acute at the inner ends, close.

Stem white, not changing color, somewhat pruinose, tapering downward, stuffed, 3-4 cm. long, 1-2 cm. thick.

Taste tardily peppery.

Odor none.

Spores globose, 6-9 microns in diameter, reticulate, white in mass.

Cystidia rather abundant.

8. *Russula lepida* Fr.

Pileus 4-10 cm. broad, *rigid*, convex, then expanded-depressed, cuticle adnate, and disappearing on disk, *unpolished*, soon *dry*, rose-red to pale blood-red, fading, disk soon pallid or variegated with paler yellowish-reddish hues, sometimes rimulose-cracked or rugulose on disk, margin obtuse, not striate.

Flesh compact, white or reddish under the cuticle, thick, abruptly thin on margin.

Gills narrowed behind and narrowly adnate or almost free, close, *rather narrow*, broader and rounded in front, *white then whitish*, few shorter, occasionally forked.

Stem 4-7 cm. long, 1-2 cm. thick, equal or slightly tapering downward, *white or tinged rosy-pink*, spongy-stuffed, rather rigid, obscurely wrinkled.

Taste *mild*, sometimes slightly bitterish, subacid.

Odor none or very slightly disagreeable.

Spores subglobose, 7-8 x 9-10 microns, reticulate, white in mass.

Cystidia moderately abundant, subcylindrical, 70-75 x 10-12 microns.

9. *Russula foetentula* Pk.

Pileus 3-7 cm. broad, soon fragile, at first subhemispherical then convex to plane and depressed, *viscid*, livid-ochraceous, russet-tinged, disk darker and innately granular, long tuberculate-striate, margin at first incurved.

Flesh thin, whitish.

Gills adnexed or nearly free, close, rather narrow, broader in front, thin, whitish, *often spotted or stained reddish*.

Stem 2.5-5 cm. long, 6-12 mm. thick, subequal, somewhat firm, spongy-stuffed, soon cavernous, whitish or sordid-white, *stained at base by cinnabar-red stains*.

Taste very slightly acrid.

Odor none or somewhat like oil of bitter almonds, varying in intensity.

Spores 6-7 x 7-9 microns, echinulate, creamy-white in mass.

Cystidia moderately abundant.

10. *Russula pectinatoides* Pk.

Pileus 3-7 cm. broad, rather firm, becoming fragile, thin, convex, then plano-depressed, viscid when moist, covered by a thin separable pellicle, radiately rugose-striate on the margin, often half way to the center, or *strongly tubercular-striate*, dingy straw color, brownish, yellowish-brown or umber-brown.

Flesh white, thin, becoming fragile, slightly *ashy under the cuticle*, not changing.

Gills whitish, close to subdistant, thin, distinct, equal, moderately broad, broadest in front, narrowed behind, often stained or broken half way from stem, some forked at base.

Stem 2-5 cm. long, 5-1 cm. thick, white or dingy, subequal glabrous, *spongy-stuffed, then hollow*, even.

Taste mild or slightly and tardily acrid.

Odor not noticeable.

Spores subglobose, 6-8 microns, echinulate, white in mass.

Cystidia few.

11. *Russula subpunctata* Kauff.

Pileus 2-5 cm. broad, *rigid*, convex then expanded-plane to depressed, cuticle adnate and scarcely separable on margin, subviscid, soon dry, *pale dull red to rosy red*, often white-spotted where cuticle disappears, minutely *rivulose* or *subgranular*, margin even, acute.

Flesh compact, firm, rather thick on disk, abruptly thin on margin.

Gills adnate to subdecurrent, thin, slightly alternate at both ends, not broad, close to subdistant, whitish, then *pale, cream-colored*, few short or forked at base, pruinose, intervenose.

Stem 2-4 cm. long, 4-10 mm. thick, subequal or tapering down, spongy-stuffed, becoming cavernous, white or rosy-tinged, unchanging, attached at times to roots and forming mycorrhiza.

Taste quickly and very acrid.

Odor none.

Spores subglobose, 7-9 x 9-11 microns, reticulate, *creamy white in mass*.

Cystidia abundant, subcylindrical, 90-110 x 8-12 microns.

12. *Russula variata* Banning and Pk.

Pileus 5-12 cm. broad, fleshy, firm, convex then depressed to subinfundibuliform, viscid, *not striate*, purplish or *deep rose pink when*

young, later variegated with olive or dark umber, or sometimes *greenish* with only a trace of *purple*, opaque and reticulate-wrinkled under lens, the thin pellicle slightly separable on the thin margin, with a subsilky or dull lustre when dry.

Flesh white, firm, cheesy, tinged grayish under pellicle.

Gills shining and persistently white, adnate-decurrent, thin, *rather crowded*, narrowed at both ends, not broad, *subdichotomously forked*, interspaces venose.

Stem 4-7 cm. long, 1-3 cm. thick, white, firm, solid, equal or subequal, sometimes tapering downward, even.

Taste mild to tardily acrid or slightly astringent.

Odor none.

Spores subglobose, 6-7 x 9-10 microns, echinulate with very fine reticulations, white in mass.

Cystidia few and short.

13. *Russula atropurpurea* Maire

Pileus 5-14 cm. broad, rigid, medium to large size, convex then plane, soon depressed, rather firm, viscid, pellicle adnate and scarcely separable on the margin only, scarlet to dark crimson when fresh and young, *becoming darker to purplish when mature or on dying*, pruinose, disk often darker, sometimes blackish, red to livid olivaceous purple, sometimes yellow spotted; margin even or only slightly striatulate in age.

Flesh dark red under the pellicle, white elsewhere, not changing to ashy.

Gills white, dingy in age, rather narrow, close behind, subdistant in front, adnexed, few short, interspaces venose.

Stem 4-7 cm. long, 1-3 cm. thick, subequal, medium stout, white with a dull lustre, *pruinose*, even, spongy-stuffed, apex floccose-punctate.

Taste acrid.

Odor none.

Spores oval, 8-10 microns, reticulate, white in mass.

Cystidia numerous.

This is the form described under this name by Kauffman. *R. atropurpurea* as used by Burlingham and others seems to be quite distinct. See note under *R. xerampelina*.

14. *Russula xerampelina* Fr.

Pileus 5-10 cm. broad, firm, convex then plano-depressed, dry or very slightly viscid in wet weather; pellicle hardly separable; not

striate on margin; surface glabrous or subpruinose, purplish-red to purplish-olive, disk olivaceous variegated.

Flesh compact, whitish then dingy.

Gills creamy, *creamy-white to creamy-yellowish*, then sordid, rather close, adnexed, moderately broad throughout, thickish, often forked, shorter ones usually intermingled, interspaces venose.

Stem white or rosy-tinged, soon dingy olivaceous-yellowish where handled, 5-7 cm. long, 1.5-2.5 cm. thick, firm, subventricose or equal, spongy-stuffed, even or obscurely wrinkled, changing where bruised to dirty *ochraceous-brown*.

Taste mild.

Odor disagreeable with age or when dying.

Spores subglobose, 7-8 x 9-10 microns, echinulate with a few reticulations, *creamy-yellowish* in mass.

Cystidia present, not extending much beyond basidia.

I include in this species forms that grade into *R. squalida* Pk. and *R. atropurpurea* Pk. since I fail to find in our specimens any sharp distinctions which seem to justify separation.

15. *Russula ochrophylla* Pk.

Pileus fleshy, firm, convex, becoming nearly plane or slightly depressed in the center, 5-10 cm. broad, surface purple or dark-purplish-red, dry, cuticle not easily separable, unpolished, glabrous, margin even, rarely very slightly striate when old.

Flesh white, purplish under the adnate cuticle.

Gills yellowish at first, becoming bright ochraceous-buff when mature, pruinose, equal, few forked at the stipe, venose-connected, subdistant, adnate.

Stem reddish or rose-tinted, paler than the pileus, white in one variety, solid, spongy within, equal or nearly so, 3.5-6.5 cm. long, 1-2 cm. thick.

Taste mild, edible.

Odor none.

Spores globose, 10 microns, echinulate with a few reticulations, bright ochraceous in mass.

Cystidia moderately abundant, rather short.

16. *Russula decolorans* Fr.

Pileus 5-12 cm. broad, *often large*, firm, globose at first then convex and plano-depressed, *orange-red* usually ochre on disk and dark

red on margin, pellicle separable, subviscid, margin even, slightly striate in age.

Flesh white, *becoming cinereous with age*, or where broken, becoming fragile.

Gills pale yellowish-ochraceous at maturity, white at first, thin, fragile, moderately broad, close, adnexed, forked at base, few short.

Stem 5-12 cm. long, 1-2.5 cm. thick, *stout*, long spongy or solid, wrinkled-rivulose, white, *the flesh becoming cinereous with age or where bruised*.

Taste mild.

Odor none.

Spores subglobose, 7-9 microns, reticulate, pale ochraceous-yellow in mass.

Cystidia very numerous.

17. *Russula flava* Romell

Pileus 5-8 cm. broad, *rather fragile*, convex, then plano-depressed, even or *slightly striate in age*, dry in dry weather, somewhat viscid when moist, pellicle separable, *dull yellow*, color hardly fading, but sometimes ashy, discolored in age.

Flesh white becoming cinereous with age.

Gills white at first, becoming yellowish, broadest towards front, narrowly adnate, close, distinct, becoming slowly gray in age.

Stem chalk-white at first, the flesh becoming ashy, equal or sub-equal, spongy-stuffed, obscurely reticulate-rivulose, rather fragile, 6-8 cm. long, 1-2 cm. thick.

Taste mild.

Odor none.

Spores globose, 8-9 microns, echinulate with a few reticulations, yellowish in mass.

Cystidia present, rather short.

18. *Russula obscura* Romell

Pileus 4-7 cm. broad, rather pliant, convex then plano-depressed, dull, *dark blood-red*, pileus sometimes blackish on disk, thin, the pellicle continuous and separable, hardly viscid when moist, *sub-pruinose* when dry, even or slightly striate in age.

Flesh whitish, becoming ashy.

Gills white at first, then dingy straw-color, moderately broad, narrowly adnate, close, mostly forked at base, equal, interspaces sometimes venose.

Stem white, becoming ashy or blackish, rarely tinged red, subequal, 4-6 cm. long, 10-15 mm. thick, spongy-stuffed, rigid, soon soft, obscurely wrinkled.

Taste mild.

Odor none.

Spores subglobose to ovate, 7-8 x 8-10 microns, echinulate, pale ochraceous in mass.

Cystidia rather numerous, subulate.

19. *Russula rubescens* Beards.

Pileus 4-10 cm. broad, firm, becoming fragile, convex-plane, *dull red, variegated* with yellowish, ochraceous or olivaceous-purplish hues, at first darker, fading, pellicle adnate, dry, scarcely separable and substrate on the margin, subglabrous, margin acute at first.

Flesh whitish, *staining slowly red then black where wounded*, becoming cinereous with age.

Gills narrowly adnate, broader in front, close to subdistant, medium broad, *equal*, rarely forked, white at first then pale creamy-ochraceous, intervenose.

Stem 3-7 cm. long, 1-2.5 cm. thick, subequal or tapering down, spongy-stuffed, glabrous, even, white, becoming cinereous in age, *changing slowly* to red then blackish where bruised.

Taste mild.

Odor none.

Spores globose, 7-10 microns, echinulate, pale ochraceous in mass.

Cystidia few and short, subhymenium not differentiated.

This species is very abundant in the vicinity of Iowa City.

20. *Russula borealis* Kauff.

Pileus 5-9 cm. broad, *firm and rather compact*, convex then plano-depressed, outline broadly elliptical, often with a sinus on one side, blood-red, disk darker or color uniform and not fading, pellicle somewhat separable, hardly viscid, margin even or obscurely striate.

Flesh white, red under the cuticle, not very thick.

Gills ochraceous, subdistant or moderately close, medium, broad, broader in front, narrowly adnate, rather distinct, edge often reddish anteriorly, equal, a few forked toward base, interspaces venose.

Stem mostly white, tinged red in places; *firm*, spongy-stuffed, thickened below, 5-7 cm. long, 1.5-2 cm. thick.

Taste mild, sometimes slightly and tardily acrid.

Odor none.

Spores subglobose, 7 x 9.5 microns, echinulate with few reticulations, deep ochraceous-yellow in mass.

Cystidia few and pointed.

21. *Russula alutacea* Fr.

Pileus 8-15 cm. broad, large, firm, convex then depressed, with dull colors, dark reddish-purple, sordid red, sometimes mixed with other shades, the reddish color predominating, with somewhat separable pellicle, glabrous, somewhat viscid in wet weather, soon dry, *pruinose and subgranulose*, margin even or somewhat short-striate in age.

Flesh white thick.

Gills *ochraceous from the beginning*, deeper ochraceous to tan-colored when mature, *rather broad*, thick, *subdistant*, broader in front, rounded adnexed, of *equal length*.

Stem 7-10 cm. long, 3-4 cm. thick, very *firm, stout*, solid, *tinged red* or entirely white, subequal or ventricose, almost even.

Taste mild.

Odor none or pleasant.

Spores subglobose, 9-11 microns, echinulate, ochraceous-yellow to alutaceous in mass.

Cystidia present.

22. *Russula nauseosa* Fr.

Pileus broadly convex, becoming plane to depressed, up to 5 cm. broad, surface purple-brown at the center, shading to garnet-brown or dull garnet toward the margin, sometimes becoming pale, viscid when wet, with the pellicle separable, glabrous, margin becoming tuberculate-striate or furrowed.

Flesh white, fragile.

Gills light yellow, then dingy ochraceous, with a few shorter ones intermingled here and there, adnexed, ventricose, somewhat distant.

Stem white, up to 2.5 cm. long, and about .8 cm. thick.

Taste mild, but somewhat nauseous.

Odor disagreeable with age.

Spores 8-9 microns in diameter, echinulate, yellow in mass.

Cystidia present.

23. *Russula emetica* Fr.

Pileus 5-10 cm. broad, fleshy, *soon fragile*, convex to plano-depressed, *rosy to blood-red*, sometimes faded to white, pellicle separ-

able, *margin strongly tubercular-striate* or even sulcate, viscid and shining.

Flesh white, *red under the cuticle*.

Gills pure white, subdistant to close, distinct, rather broad, equal, broadest toward front, narrowly adnexed or free, interspaces venose.

Stem 4-7 cm. long, 1-2 cm. thick, white or tinged red, subequal, spongy-stuffed, even.

Taste very acrid.

Odor none.

Spores subglobose to globose, 7.5-10 microns, reticulate, white in mass.

Cystidia numerous.

Our specimens of this species are usually small. The pilei, rarely, if ever, reach a diameter of 10 cm.

24. *Russula fragile* Fr.

Pileus 2.5-5 cm. broad, *very thin* and fragile, convex then plano-depressed with a thin viscid pellicle, tubercular-striate on the thin margin, glabrous, rather uniform rosy or pale red, sometimes faded or bleached to white.

Flesh *white under the pellicle*, thin.

Gills white, thin, crowded, adnexed, ventricose, moderately broad.

Stem 2.3-5 cm. long, .5-1 cm. thick, white, spongy then hollow, equal, fragile.

Taste promptly and very acrid.

Order none.

Spores subglobose, 8-9 microns, echinulate with a few reticulations, white in mass.

Cystidia very numerous and rounded.

25. *Russula fallax* Cke.

Pileus 3-7 cm. broad, *thin, fragile*, color incarnate or pale rose, the disk pale *olivaceous or livid*, sometimes darker or purplish, soon plane or slightly depressed on the disk, quite viscid, margin striate and becoming elevated, surface faintly rugulose under lens.

Flesh white.

Gills white, unchanged, subdistant, attached by a point, *narrow, edge even*.

Stem 3-4 cm. long, 6-10 mm. thick, pure white, cylindrical or compressed, equal, spongy-stuffed, soon hollow.

Taste promptly and very acrid.

Odor none.

Spores subglobose, 7-9 x 9-10 microns, reticulate, white in mass.

Cystidia present, short.

26. *Russula albidula* Pk.

Pileus 2-5 cm. broad, *white*, broadly convex, glabrous, pellicle *viscid* and separable when fresh, margin even.

Flesh white, subfragile.

Gills white, moderately crowded, adnexed, not broad, of equal length, some forking at base, interspaces venose.

Stem 2.5-4 cm. long, 8-12 mm. thick, white, equal, spongy-stuffed, even.

Taste acrid.

Odor none.

Spores subglobose, 7-10 microns, reticulate, white in mass.

Cystidia present, rather few.

27. *Russula sanguinea* Fr.

Pileus 3-6 cm. broad, rather firm at first, subfragile, convex-plane or depressed, *rosy-red*, viscid, margin acute and thin, pellicle subadnate, easily separable on margin and tubercular-striate.

Flesh rather thin, white, red under pellicle.

Gills slightly adnate, close to subdistant, *equal*, not broad, *creamy-white*.

Stem 4-6 cm. long, subequal or tapering downward, often eccentric, *white or tinged rosy-red*, spongy-stuffed then cavernous, rather fragile, glabrous, even.

Taste tardily but truly acrid.

Odor none.

Spores globose, 8-10 microns, echinulate, creamy-white in mass.

Cystidia present, few.

28. *Russula corinthiirubra* Burl.

Pileus becoming plane or slightly depressed in the center, up to 9 cm. broad, surface Corinthian-red, fading, the center becoming tinged with maize-yellow, viscid, with the pellicle separable half way to the center, glabrous, margin becoming slightly striate-tuberculate.

Flesh white, tinged red next to pellicle.

Gills becoming yellow, equal, some forked next to the stipe, venose-connected, narrow at the inner ends, broad and ventricose toward the outer; rather thick, close.

Stem white, firm, nearly equal, 4 cm. long, 1.7 cm. thick.

Taste slowly acrid.

Odor none.

Spores subglobose, 7-8 x 9-10 microns, reticulate, ochraceous in mass.

Cystidia very numerous, rounded at tip.

29. *Russula tenuiceps* Kauff.

Pileus 7-12 cm. broad, thin, fragile, convex to expanded, the somewhat viscid pellicle easily separable, margin at first connivent, *striate*, deep rosy or blood red, sometimes white, spotted or tinged with orange blotches, sometimes uniform red, with or without minute rugæ.

Flesh white, red under cuticle, *very fragile at maturity*.

Gills white, then yellow-ochraceous, crowded, narrow, fragile, narrowly adnate to free, few forked, interspaces venose, equal.

Stem fragile, white or rosy-tinged, spongy-stuffed, subequal or ventricose, obscurely rivulose, white within and unchanged, 5-9 cm. long, 2-2.5 cm. thick.

Taste acrid, sometimes tardily but very acrid.

Odor not marked.

Spores subglobose, 6-9 x 8-11 microns, echinulate, yellow-ochraceous in mass.

Cystidia present.

30. *Russula veteriosa* Fr.

Pileus 5-7.5 cm. broad, convex then expanded, with a somewhat separable pellicle, *indistinctly striate* on the margin, deep rose-red, viscid when moist.

Flesh white, red under the cuticle.

Gills white at first, *then straw-color or pale ochraceous*, narrow, adnate, close, broader in front, equal or few shorter, few forked, interspaces venose.

Stem white, *never red*, equal or subequal, spongy-stuffed, somewhat slender, fragile, hollow, even, 4-5 cm. long, 1-1.5 cm. thick.

Taste very acrid.

Odor none.

Spores subglobose, 8-10 microns, echinulate, yellowish-ochraceous in mass.

Cystidia numerous.

31. *Russula subdepallens* Pk.

Pileus 5-14 cm. broad, *fragile*, convex then plane and depressed, margin elevated in age, *bright rosy-red*, shading into yellowish blotches as if the red color were put over the yellow, disk paler in old specimens, disk dark red in very young plants, with a thin separable, viscid pellicle, *tubercular-striate* on margin, obscurely wrinkled elsewhere.

Flesh white-rosy under cuticle, becoming slightly cinereous, very fragile, thin.

Gills white, broad in front, narrowed behind, adnate, subdistant, few forked, interspaces venose.

Stem white, spongy-stuffed, rather stout, 4-10 cm. long, 1-3 cm. thick, subequal.

Taste mild.

Odor none.

Spores globose, 7.5-8 microns, echinulate with fine reticulations, white in mass.

Cystidia none.

32. *Russula purpurina* Quel. and Schultz

Pileus 3-7 cm. broad, fragile, *viscid*, usually very viscid, subglobose then expanded and slightly depressed at the disk, *brilliant rosy-red to blood-red* or even darker, pellicle somewhat separable, margin thin but *not striate* except when fully expanded, surface when dry as if with a bloom.

Flesh white, red under the cuticle, thin, fragile, unchangeable.

Gills white, later dingy-white or yellowish; medium close to subdistant, adnexed, not broad, broadest in front, mostly equal, few or none forked, interspaces sometimes venose, edge floccose-crenulate.

Stem rather long, 5-8 cm. long, 8-12 mm. thick, sprinkled rosy-pink, equal or subequal, spongy-stuffed, fragile but rather soft.

Taste mild.

Odor none.

Spores subglobose to globose, 6-8 x 8-10 microns, reticulate, white in mass.

Cystidia present.

33. *Russula uncialis* Pk.

Pileus 2-5 cm. broad, thin, rather fragile, convex then expanded-depressed, *pink or bright flesh-color*, unicolorous, the rather adnate pellicle slightly separable, slightly viscid when moist, pruinose and

pulverulent when dry, margin not striate till old.

Flesh white, pink under pellicle, unchanged.

Gills pure white, scarcely changing with age, rather broad, broadest in front, narrowed behind and adnate; subdistant or moderately close, distinct, entire on edge, few forked, interspaces venose.

Stem white, rarely tinged pink, rather short, 1-3.5 cm. long, 4-10 mm. thick, spongy-stuffed, equal, glabrous.

Taste mild.

Odor none.

Spores subglobose, 7-8 microns, echinulate with a few reticulations, white in mass.

Cystidia few.

This species with us is generally fully 5 cm. broad but in other respects agrees with the descriptions.

34. *Russula integra* Fr.

Pileus 5-10 cm. broad, firm, *soon fragile*, discoid, convex or campanulate then plano-depressed, covered with a *viscid separable pellicle*, thin on the margin, at length *coarsely tubercular-striate*, variable as to color in different plants, *colors dingy or sordid*, from buff through to reddish-brown and dark dull red, *fading*.

Flesh white not changing.

Gills white at first, then creamy-yellow to buff-ochraceous, not strongly ochre, *broad, distant*, equal, nearly free.

Stem white, unchanged, never red, soon quite fragile, conic or short-clavate at first, then subequal or ventricose, spongy-stuffed, even.

Taste mild.

Odor none.

Spores subglobose, 8-9 x 9-10 microns, echinulate, creamy-yellow to pale ochraceous in mass.

Cystidia none.

35. *Russula amygdaloides* Kauff.

Pileus 4-8 cm. broad, thin, medium size, ovate at first with a straight margin, then convex-plane or depressed, very viscid, *fragile*, pale rosy-flesh color tinged with yellow, sometimes *peach color*, sometimes dull citron-yellow, varying in color from young to old, pellicle continuous and entirely separable, margin becoming strongly tuberculate-striate.

Flesh thin, white, not changing color, soft.

Gills bright ochraceous-yellow, white at first, rather narrow, broadest in front, narrowed and adnexed behind, subdistant at maturity, dusted by spores.

Stem 4-8 cm. long, 1-2 cm. thick, subequal to ventricose, soft and fragile, loosely stuffed then cavernous (but not from grubs), white, rarely tinged with delicate pink, slightly wrinkled, subglabrous.

Taste mild.

Odor none.

Spores subglobose, 7-9 microns, echinulate with very few reticulations, bright ochre-yellow in mass.

Cystidia very few.

36. *Russula flaviceps* Pk.

Pileus convex, then expanding and slightly depressed in the center, 5-10 cm. broad, surface amber-yellow to golden-yellow, viscid, with a separable pellicle, glabrous, margin even, when young, faintly striate when old.

Flesh white.

Gills white, soon becoming Naples-yellow and dusted with spores, equal, simple, adnate or slightly rounded next to the stipe, broader at the outer ends, rather narrow, close.

Stem white, equal or nearly so, stuffed or spongy within, 4-6.5 cm. long, 8-12 mm. thick.

Taste mild or slightly acrid.

Odor none.

Spores subglobose, 8-9 x 9-10 microns, echinulate, maize-yellow in mass.

Cystidia very few.

37. *Russula chamæleontina* Fr.

Pileus 2-5 cm. broad, *rather small*, fragile, thin, plano-depressed, with a viscid separable pellicle, margin even at first then striatulate, *color varying for different pilei*, mostly same shade of red, purple, etc., fading to yellowish especially on disk.

Flesh white, thin.

Gills thin, crowded or close, adnexed or almost free, equal, rather broad, sometimes almost narrow, few forked, interspaces venose, ochraceous or ochraceous yellow.

Stem 2-5 cm. long, 4-6 mm. thick, white, spongy-stuffed then hollow, *slender*, equal or subequal to subventricose, sometimes subclavate, even or obscurely rivulose.

Taste mild.

Odor none.

Spore subglobose to globose, 6-8 x 8-10 microns, echinulate with a few reticulations, ochraceous in mass.

Cystidia present.

38. *Russula humidicola* Burl.

Pileus broadly convex, soon becoming depressed in the center, up to 6 cm. broad, surface varying in color from salmon, reddish-salmon, and yellowish salmon to Morocco-red in the center, sometimes fading, viscid, with pellicle separable except on disk, glabrous, margin drooping, soon tuberculate-striate.

Flesh thin, white fragile.

Gills white, becoming cream-colored, equal, rarely forking next to the stipe, interveined, acute, narrow and nearly free at the inner ends, broad and rounded at the outer, close, thin, pruinose.

Stem white, nearly equal, spongy, then hollow, 3-5 cm. long, 5-10 mm. thick.

Taste mild.

Odor none.

Spores globose to elliptic, 5-6 x 7 microns, echinulate with few reticulations, maize-yellow in mass.

Cystidia present, short and blunt.

39. *Russula luteobasis* Pk.

Pileus convex, then nearly plane, 2.5-8 cm. broad, surface at first rosy or red, then paler; yellowish in center, viscid when wet, cuticle separable, glabrous, margin even, indistinctly striate when old.

Flesh white or whitish.

Gills white to cream-yellow or pale-ochraceous when old or in drying, equal, not forking, except near the stipe, adnexed to adnate, rather close, broad.

Stem white, yellow to orange-yellow at base, subequal, stuffed, 2.5-7 cm. long, .4-2 cm. thick.

Taste mild.

Odor none.

Spores subglobose, 7-8 x 8-9 microns in diameter, reticulate, yellow-ochraceous in mass.

Cystidia none.

40. *Russula roseipes* (Secr.) Bres.

Pileus 2.5-5 cm. broad, *thin, fragile*, convex then plano-depressed, with a viscid, separable pellicle, margin tubercular-striate when mature, soon dry, *rosy-red* or *flesh-red*, disk tending to ochre-yellowish.

Flesh white, thin, unchanged.

Gills soon truly ochraceous, subdistant, mostly equal, broadest in front, ventricose, narrowly adnate or almost free, few forked, interspaces venose.

Stem white and rosy-sprinkled, stuffed then cavernous, equal or tapering upward, even, 2.5-5 cm. long, 5-12 mm. thick.

Taste mild.

Odor none or pleasant.

Spores subglobose to globose, 7-8 x 9-10, microns, echinulate with few reticulations, ochraceous in mass.

Cystidia none.

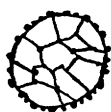
BIBLIOGRAPHY

1. Beardslee, H. C., The Russulas of North Carolina. Jour. Elisha Mitchell Sci. Soc. 33: 147-197, 1918.
2. Burlingham, G. S., Russula. In N. A. Flora. 9: 201-236, 1915.
3. Kauffman, C. H., Agaricaceæ of Michigan, 1918.
4. Melzer, V., L'ornementation des spores de Russula. Bull. soc. Myc. France. 40: 78-81, 1924.
5. Persoon, C. H., Synopsis methodica fungorum. 438-447, 1801.
6. Shimek, B., Plant Geography of the Lake Okoboji region. Bull. Lab. Nat. Hist., Univ. of Iowa. 7: 1-90, 1915.

EXPLANATION OF PLATE

Spores of Russula

- | | |
|-----------------------------|------------------------------|
| 1. <i>R. albidula</i> | 21. <i>R. nigricans</i> |
| 2. <i>R. alutacea</i> | 22. <i>R. obscura</i> |
| 3. <i>R. amygdaloides</i> | 23. <i>R. ochroleucoides</i> |
| 4. <i>R. atropurpurea</i> | 24. <i>R. ochrophylla</i> |
| 5. <i>R. borealis</i> | 25. <i>R. pectinatoides</i> |
| 6. <i>R. chamæleontina</i> | 26. <i>R. purpurina</i> |
| 7. <i>R. corinthiirubra</i> | 27. <i>R. raoultii</i> |
| 8. <i>R. crustosa</i> | 28. <i>R. roseipes</i> |
| 9. <i>R. decolorans</i> | 29. <i>R. rubescens</i> |
| 10. <i>R. emetica</i> | 30. <i>R. sanguinea</i> |
| 11. <i>R. fallax</i> | 31. <i>R. subdepallens</i> |
| 12. <i>R. flava</i> | 32. <i>R. subpunctata</i> |
| 13. <i>R. flaviceps</i> | 33. <i>R. tenuiceps</i> |
| 14. <i>R. fœtentula</i> | 34. <i>R. uncialis</i> |
| 15. <i>R. fragilis</i> | 35. <i>R. variata</i> |
| 16. <i>R. humidicola</i> | 36. <i>R. veternosa</i> |
| 17. <i>R. integra</i> | 37. <i>R. virescens</i> |
| 18. <i>R. lepida</i> | 38. <i>R. viridella</i> |
| 19. <i>R. luteobasis</i> | 39. <i>R. xerampelina</i> |
| 20. <i>R. nauseosa</i> | |



1



2



3



4



5



6



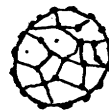
7



8



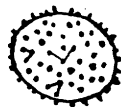
9



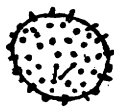
10



11



12



13



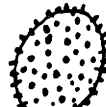
14



15



16



17



18



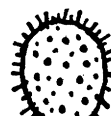
19



20



21



22



23



24



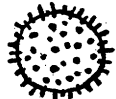
25



26



27



28



29



30



31



32



33



34



35



36



37



38



39

OCCURRENCE OF MYCORRHIZA IN IOWA FOREST PLANTS

M. L. LOHMAN

INTRODUCTION

The root-fungus association in the higher plants has had attention in botanical literature since the middle of the nineteenth century. The classical investigations of Kamienski (1881), Frank (1885), and Stahl (1900) gave an impetus to this phase of mycological and physiological research which has resulted in a continuous series of papers up to the present time. Most investigations have been made by European workers, and the most recent studies are those of Demeter (2), Melin (9, 10, 11, 12, 13), and Peyronel (17) on the continent, and Rayner (18, 19, 20, 21) in England.

The term "mycorrhiza" was first used by Frank (3) to designate that condition of a fungus-root system in which the fungus mycelium forms a web of interwoven hyphæ about the root-tips of the higher plants. This term was adopted by later workers and it is the accepted term to-day, although it has been extended to include those conditions in which the fungus hyphæ are present in parts other than the root, or throughout the entire plant. The term "mycotrophic" has been suggested as more accurate, especially when applied to such plants as *Corallorrhiza*, in which there are no roots (Skene, 22). "Mycorrhiza" has also been used quite loosely by some writers to imply in one instance the fungus-root system, and in others the fungus alone, which, of course, is misleading and incorrect.

The technique involved is complicated, and it is exceedingly difficult to identify the fungus found in mycorrhizal relationship with the root of a particular plant. Considerable care must be exercised to succeed in getting the fungus in culture.¹ Whether in culture or not, not all mycorrhizal fungi produce fruit bodies, but the mycelium may remain sterile in the soil for years, continuing to form mycorrhiza. The method of tracing the mycelium from the fruiting body, through the soil, to the root of the higher plant has been employed as a means of identification, but it is

¹ See Rayner (18) for culture methods.

believed that such methods allow considerable opportunity for error. Paulson (16) states that the bulk of mycorrhiza is found in decaying leaves near the surface layers where decomposition is not far advanced. Thus the soil is permeated with the mycelium of soil fungi, many of which form mycorrhizal connections with the higher plants.

TYPES OF MYCORRHIZA

In most literature the types of mycorrhizal development are given as ectotrophic and endotrophic, signifying respectively that the fungus is growing on the outside or on the inside of the root of the higher plant. A third quite peculiar type of development has been reported, i.e., those endotrophic forms developing the characteristic vesicles and arbuscles. Rayner (20) believes the distinction between ectotrophic and endotrophic forms is in the degree of infection of the root by the fungus. This suggests a possible transition on the part of a mycorrhiza-forming fungus from the endotrophic character to the ectotrophic, and that a given fungus may be endotrophic with one plant, and ectotrophic with another. It is possible that a mycorrhiza-forming fungus of a general endotrophic habit may form vesicles or arbuscles in one plant, and not in another (Demeter, 2).

The ectotrophic form (fig. 46, pl. 8) is readily noted since it occurs commonly in connection with the roots of many common forest trees such as beech and oak, also pine, larch and other conifers, the root having a coral-like appearance, being short, thickened, profusely branched, and with root hairs usually lacking or few. This was the type noticed by Frank which led to his further investigations. He regarded the outer part of the root simply as a fungus sclerotium, and described it as a pseudoparenchymous-like layer, formed by the massed hyphæ, resulting in a thick mantle or weft of fungus mycelium about the root of the higher plant. The fungus sends haustoria in between the epidermal cells, and these penetrate the root between the outer cortical cells. Melin (1921) has shown for pine and spruce that infection in this ectotrophic form takes place through the root hairs or epidermal layer of cells, and that the fungus first exists inside the cortical cells, but after digestion commences, the hyphæ pass between the cells of the epidermis and form the typical mantle.

In the endotrophic mycorrhiza (15) the hyphæ penetrate the

root and develop within the cortical cells, obtaining nourishment there. In such cases the mycelium may be intercellular, intracellular, or both, as observed by West (24) in mycorrhiza of the Marattiaceæ. The fungus in many forms of endotrophic mycorrhiza is thought to be a Phycomycete or a closely allied form. Peyronel is of the opinion that the mycelium of these phycomycetoid endotrophs forms in humus soil a continuous network which involves the root-system of the higher plants, passing from one to another, and also that these phycomycetoid endotrophs live a saprophytic existence, continuing their existence and development in the cortical tissues of the root after the death of the latter. In most endotrophic mycorrhiza the fungus forms haustorium-like arbuscles and spore-like vesicles (17), both of which will be discussed later. This type seems to differ sharply from the endotrophic mycorrhizal fungus of the orchids which has been isolated and cultivated, and is regarded as belonging to the genus *Rhizoctonia*.

Rayner (18, 19, 20) has worked with an endotrophic fungus in *Calluna vulgaris* which affects all parts of the plant; root, stem, leaf, flower, and fruit. The distinction made by her between ectotrophic and endotrophic forms is one of degree of infection only. The hyphæ on entering the root cell seem to be attracted towards the nucleus. Branching then occurs and the cells are filled with large hyphæ which are capable of absorbing material from the cell as well as from the external mycelium.

In many endotrophic mycorrhiza, especially when the mycorrhizal fungus suggests a Phycomycete, the peculiar vesicles and arbuscles (figs. 44 and 45, pl. 8) first described by Gallaud (4) are found. Peyronel (17) has observed these structures in endotrophic fungi, not, however, in orchids, and he believes the fungus concerned to be a Phycomycete, close to the genus *Endogone*. West (24) reports their presence in the mycorrhiza of the Marattiaceæ. A complete discussion of these forms is given by Demeter (2) in connection with his studies on the mycorrhizal fungus of *Vinca minor*, *Vincetoxicum officinale*, and *Asclepias cornuti*. He believes the fungus in these species to be the same as that found in the orchids, but in these species it develops the vesicles and arbuscles. Apparently these peculiar endotrophic structures have nowhere been reported for the orchids. Terminal and intercalary vesicles may form on either intercellular or intracellular hyphæ, and appear to be storage organs. But more important than the vesicles, according to Deme-

ter are the tree-like structures which Gallaud termed "arbuscles." These arbuscles are formed by a cloud of fine granules about the tips of the fungus branches. These are regarded by Demeter as apparently a protein precipitate formed by the mixing of the protoplasm of the cell of the higher plant and that of the fungus when the tips of the fungus branches burst. The granules later diffuse throughout the cell, and finally unite to form organized bodies—the so-called "sporangioles." He suggests the name "Plasmoptysiomycorrhiza" for this type of fungus.

Magrou (8) found vesicles in the endotroph of the wild potato and arbuscles in the fungus of *Mercurialis annua*. Upon inoculating *Solanum tuberosum* with *Mucor solani* he obtained terminal and intercalary vesicles resembling very much those of the endotroph found in nature.

SYMBIOSIS IN MYCORRHIZAL CONNECTION

Several theories have been advanced concerning the nutritive relation existing in mycorrhiza, and in connection with each a considerable amount of experimental evidence has accumulated. It is still a question as to whether a mycorrhizal fungus is in any way parasitic on the higher plant, or whether there is established a state of true symbiosis, and if so, in what way the higher plant benefits by the presence of the fungus. It is undoubtedly true that no one rule can be set down for mycorrhiza in general, and that this physiological relationship varies between different plants and the same fungus; and between different fungi with the same plant. In any case there is probably a time in mycorrhizal development when the relationship is parasitic, and when it is symbiotic. In other words, such a physiological relationship is highly variable.

Magrou (8) defines symbiosis as that condition where both participants (higher plant and fungus) are in an equal state of reciprocity. The plants resist the attack of the fungus by some mechanical means of rendering themselves immune, such as the suffocation of the fungus by the development of cell structure. Miehe (14) believes that the fungus on *Casuarina equisetifolia* is a typical symbiont, changing nitrogenous materials already derived from the soil into such forms as can be used by the plant.

Molisch (15) in discussing the general physiological conditions states that perhaps the fungus simply assimilates free nitrogen as do the nodule-bacteria in the Leguminosæ, or that it aids in the

nutrition of the higher plant to some extent by making undigestible humus materials digestible, the plant thus obtaining nourishment through the fungus. In such cases the fungus also obtains organic material from the plant. He also suggests the idea that the fungus digests itself, and that the higher plant may in this way assimilate organic and inorganic materials. Whether or not soil fungi definitely assimilate free nitrogen is still a problem for research, although some positive and a considerable amount of negative evidence has been obtained (5, 22).

Rayner (19) in discussing the nutrition of mycorrhizal plants in connection with the endotroph of *Calluna vulgaris* states emphatically that the fungus has the general appearance of a parasite, and can act as such under certain conditions. She concludes that the reciprocity involved in the formation of active mycorrhiza as represented in *Calluna vulgaris* marks a relatively advanced stage of relationship, implying an extremely intimate association, and resulting in a "balance-of-profit" for the higher plant. The view put forward by the same author (18) in discussing the obligate symbiosis in *Calluna vulgaris*, is that the first step towards the formation of mycorrhiza involves a temporary modification of the parasitic habit on the part of the fungus concerned.

Melin (11, 13) upholds the fungus-symbiont theory for the plants with which he has worked. He believes that various symbionts of forest trees may enable their partners to assimilate the different organic nitrogenous compounds of the soil with a varying degree of ease, and that certain species of fungi can utilize the complex albumin bodies of the humus layer better than their disintegration products; while others more readily assimilate the latter. Melin produced ectotrophic mycorrhiza in culture on the birch with *Boletus scaber*, and on the ash with *B. rufus*. The relationship ascribed is pure symbiosis, the higher partner deriving much food from the digestion of the hyphæ of the mycorrhizal fungus.

The establishment of a state of true symbiosis is referred to by Thomas (23) in his paper on the genus *Corallorrhiza*, and recent work by Melin (10) has led the latter to believe that in many cases the higher plant and the fungus do live in a true state of symbiosis, both the fungus and the higher plant being benefited by this close morphological and physiological association. He bases his conclusion, first, on results of synthetic culture experiments; second,

on observations made under natural conditions; and third, on anatomical structure of the mycorrhiza.

It was long believed that the fungus relationship in the orchids was one of true mycosymbiosis, and that the fungus was absolutely essential to germination and growth of the orchid. Knudson (7) has demonstrated recently that the germinating orchid seed is benefited by the presence of the fungus in that the fungus increases the hydrogen-ion concentration, and changes complex carbohydrates into forms more available. Uninfected seeds, in solutions with an acidity equivalent to that produced by the fungus, germinated just as well as infected seeds in control solutions which were less acid, and in which uninoculated seeds would not germinate. His uninoculated control cultures had a pH value of 5.7, and on inoculation of such cultures with the fungus the acidity was increased so that the pH value ranged from 4.2 to 4.4.

Thus, in general, it may be said that the early workers believed that there was a state of true reciprocity existing between the higher plant and the mycorrhizal fungus. There was then a period in which the theory of parasitism on the part of the fungus was advanced, followed by more recent work in which the relationship was again thought to be one of true symbiosis as defined by Melin.

METHODS USED IN COLLECTION AND PREPARATION FOR STUDY

The purpose of this research was to make as extensive a survey as possible, in the time at my disposal, of the occurrence and nature of mycorrhiza in Iowa forest plants. Thus the methods used in collecting, preliminary study of roots and soil, fixing, and staining, were those most convenient for use in such a survey. The intention was to examine and study the roots of as many plants belonging to representative families as possible, without intensive study of any one particular plant.

All but one of the collections were made from April to October, 1925. The exception was an abundant supply of *Corallorrhiza*, collected in September, 1924. Collections were made in the typical Iowa forests of the river valleys of Johnson and Iowa counties, and in the forests of the lake borderlands of Dickinson County, with a few collections from open plant associations about West Okoboji Lake. Plants collected in the field were taken into the laboratory with a considerable quantity of soil attached, the pH reading of the

soil solution was made, and the plants were then placed in the refrigerator until the preliminary examination could be made.

The pH values of the soil solutions were determined as soon as the material was brought from the field. Experiment showed that a reading of the hydrogen-ion concentration of the soil solution in the field was not necessary, and that soils kept in the refrigerator for from twenty-four to thirty-six hours exhibited surprisingly little variation in the pH reading from that taken in the field, or immediately upon arriving at the laboratory, which was rarely more than four hours from the time of collection. In obtaining the pH value, about 5 cc. of soil was well mixed by shaking in a test tube with 20 cc. of neutral distilled water. This was allowed to stand until the turbidity of the soil solution was considerably reduced, ten to fifteen minutes being sufficient. The determination of the hydrogen-ion concentration was made with the standard indicators to one decimal place. Such a method, of course, is not free from error, but in general the error involved was compensating, and the relative acidity or alkalinity of the various soils tested was sufficiently accurate for the purposes of such a survey. In general, the soil taken for the pH reading was that about those roots exhibiting the usual external characteristics of mycorrhiza, or, in plants which did not disclose mycorrhiza in external appearance of the roots, the soil sample was usually taken at a depth of several inches. In several collections, as a matter of experiment, pH readings of the soil solutions were made from the surface layer, and also from various depths down to a depth of six and eight inches, and little variation in the pH values was revealed.

A preliminary examination was made on all plants collected, which involved a careful study of the external characters of the roots, and a microscopic examination of the internal structure by the study of free-hand sections. Note was taken of the general appearance, form, root-hair formation, and of any traces of fungus hyphæ found externally or internally. Free-hand sections were made across the root, beginning at the root-tip and then at intervals in the older root parts up to 3-4 cm. from the tip until no trace of fungus hyphæ was found. The staining of free-hand sections with Gram's iodine solution, or by an aqueous solution of eosin, or both, was found very useful. Roots of collections which disclosed ectotrophic or endotrophic fungus hyphæ in this examination were fixed and preserved for further study.

Several attempts were made, with the usual precautions and methods of sterilization, to obtain cultures of the ectotrophic fungus present on the roots of *Ostrya virginiana* and *Quercus macrocarpa*, but these were unsuccessful.

Chromo-acetic acid (1 per cent) was used in general as a fixing agent, although several collections were fixed and preserved in formalin-alcohol. Material fixed in chromo-acetic acid was washed, and then preserved in 5 per cent formalin solution until further study. Sections of different parts of roots of the same collection were kept in separate vials. Preserved material for microscopic study was run through the complete series of alcohols, at 10 per cent intervals, for dehydration, with four steps from absolute alcohol to pure xylol, and was imbedded in 48° paraffin. Longitudinal sections were made of roots of all plants which disclosed mycorrhiza in the preliminary examination, as a check on such findings, and cross sections were made of roots of those collections which disclosed outstanding mycorrhizal types in the longitudinal sections. The microtome sections were cut from 10 to 15 microns, the 15 micron sections being more satisfactory for this particular study. Good paraffin ribbons were obtained showing no great amount of tearing of vascular and cortical tissue in either longitudinal or cross sections of such woody roots as those of oak, ash, hornbeam, cottonwood, and the older roots of ferns, without special treatment. Land's albumin fixative as given by Chamberlain was the only material used in fixing the paraffin sections to the slide. This proved very successful in general, but surprisingly unsuccessful in the case of two ferns. In those sections of *Adiantum pedatum* which possessed an ectotrophic fungus layer of considerable thickness, the weft of fungus hyphæ did not adhere to the slide well; and in the material of *Osmunda claytoniana* which possessed an endotrophic fungus, the cells containing the disorganizing fungus hyphæ were mostly lost.

No attempt was made to experiment with various stains, but since roots of many different species of plants, and different collections of the same species were being investigated, Flemming's triple stain was used as the general stain. In this the safranin was made from equal parts of a saturated solution in 95 per cent alcohol and a saturated aqueous solution, with 1 per cent aqueous solutions of gentian violet and orange G. In cases where more careful study was desired, iron-alum hæmatoxylin counterstained with 1 per cent

aqueous solutions of orange G or erythrosin was used as a check. The hæmatoxylin proved the better stain in the case of most ectotrophic fungi, and also for those orchids which exhibited endotrophic fungus mycelium.

RESULTS

Seventy plant collections were made, forty-three of which disclosed fungi in mycorrhiza-like relationship, the other twenty-seven collections being negative. Of the collections all but one (the stock collections of *Corallorrhiza*) were made between April 13 and October 10, 1925, in Dickinson and Johnson counties, with one collection from Iowa County. The localities worked in these three counties are covered with typical Iowa forests. Most of the Johnson County collections, and the collection from Iowa County were made in the months of April and May. The temperature was practically normal for southeastern Iowa, but the rainfall until June was above the average. Conditions were favorable for an abundant fungus flora and especially for mycelial growth in the soil. Eight collections were made in Johnson County in September and October, following an extremely warm summer with a normal amount and distribution of rainfall. Warm weather continued until about October 15, when heavy frosts, early snows, and frozen ground prevented any more collecting. The ground was slightly frozen when the last collections were made.

The collections in Dickinson County were made in June and July. Cool, wet weather prevailed the latter part of June, but the month of July was very hot and dry. Dickinson County had an extremely dry spring. Conspicuous fungi were very scarce in the Okoboji region in the summer of 1925, only a few specimens of the very common genera being found during the entire summer. It is extremely probable that this was reflected in the growth and fewer numbers of soil fungi.

The total of seventy plant collections made represented twenty-one families, thirty-four genera, and forty species. The results of these collections, including field notes, the most important notes from preliminary examinations, and examinations of prepared slides, can be best correlated in tabular form. In Table I, which concerns those species in which mycorrhiza was present in all examinations, the arrangement is in phylogenetic order² according

² The nomenclature and phylogenetic order used is that of Gray's Manual of Botany; Ed. 7.

TABLE I
PLANTS IN WHICH MYCORRHIZA WERE FOUND ON EACH EXAMINATION

Species	pH of soil solution	Habitat of higher plant	Important characters of higher plant or fungus	Place of collection (county)	Date of collection
<i>Pteris aquilina</i>	6.4	oak-hickory forest; dense under-growth	ectotroph of very fine mycelium; endotroph of larger, septate hyphae;	Johnson	Oct. 10, 1925
" "	7.2	oak-hickory forest	ectotrophic weft, septate hyphae plus endotroph of same character	" "	" " "
<i>Onoclea sensibilis</i>	4.9	open edge of oak-hickory forest	ectotroph about lateral roots	" "	May 20, 1925
<i>Botrychium virginianum</i>	5.0	oak-hickory forest	large phycomycetoid endotroph; numerous arbuscles	" "	May 20, 1925
<i>Equisetum arvense</i>	5.1	sandy soil along road by east edge of woods	phycomycetoid endotroph; abundant throughout cortical cells	" "	" " "
<i>Uvularia perfoliata</i>	7.2	oak-hickory forest; north ravine	no root hairs; disorganizing endotroph in root tips	" "	Apr. 19, 1925
<i>Erythronium albidum</i>	6.2	oak-hickory forest; north ravine	large phycomycetoid endotroph	" "	" " "
<i>Smilacina racemosa</i>	6.6	oak-hickory forest; dense	few root hairs; disorganizing endotroph; with arbuscles	" "	Oct. 10, 1925
" "	7.0	oak-hickory forest; dense	root hairs present; disorganizing hyphae in cortical and epidermal cells	" "	" " "
<i>Orchis spectabilis</i>	6.8	oak-hickory forest; ravine	few root hairs; typical orchid fungus in few cells 5 mm. from tip	" "	Apr. 19, 1925
" "	5.3	coppice growth; N.E. exposure	typical orchid endotroph; more abundant; 1 to 2 mm. from root tip	" "	May 20, 1925
<i>Corallorrhiza odontorhiza</i>	-----	hornbeam thicket in oak woods	typical orchid endotroph; very abundant in subterranean parts	" "	Sept. 13, 1924
<i>Populus deltoides</i>	6.6	sandy beach 15' from water line of lake	thick ectotroph as in <i>Ostrya</i>	Dickinson	July 21, 1925
" "	6.5	" " "	usual ectotroph plus large phycomycetoid endotroph	" "	" " "
<i>Ostrya virginiana</i>	7.6	hornbeam grove, east exposure along lake shore	ectotroph forming thick mantle; endotroph present; apparently the same fungus; seedling of 1st yr.	" "	July 3, 1925

<i>Ostrya virginiana</i> (cont'd)	7.6	"	"	"	ectotroph only;	"	"	"	"	"
"	7.9	bur-oak-hornbeam	grove,	"	"	"	"	"	"	"
"		E. exposure along lake	shore	"	"	"	"	"	"	10,
"	8.0	"	"	"	"	"	"	"	"	"
"	7.9	"	"	"	"	"	"	"	"	"
"	7.2	"	"	"	"	"	"	"	"	28,
"	7.3	"	"	"	"	"	"	"	"	"
<i>Hepatica acutiloba</i>	7.2	north exposure; lime-stone	cliff	"	no root hairs; endotroph several	"	"	"	Johnson Apr. 13, 1925	"
"	6.5	north ravine; oak-hickory	forest	"	mm. from tip of root	"	"	"	"	19,
<i>Podophyllum peltatum</i>	6.8	"	"	"	root hairs abundant; large disor-	"	"	"	"	"
"		"	"	"	ganizing endotroph in root tips	"	"	"	"	"
"		"	"	"	phycomycetoid endotroph to 1.5	"	"	"	"	"
"		"	"	"	cm. from tip; in cortical and	"	"	"	"	"
"		"	"	"	epidermal cells disorganization of	"	"	"	"	"
"		"	"	"	fungus	"	"	"	"	"
<i>Caulophyllum thalictroides</i>	6.2	"	"	"	same as above; root hairs present	"	"	"	May 20, 1925	"
"	6.5	"	"	"	no root hairs; long spiralled roots;	"	"	"	Apr. 19, 1925	"
<i>Sanguinaria canadensis</i>	5.2	N.E. exposure; coppice	growth	"	large phycomycetoid endotroph	"	"	"	May 20, 1925	"
<i>Melilotus alba</i>	6.5	sandy beach, 20' from	water line of lake	"	no root hairs; ectotrophic fungus	"	"	"	Dickinson July 20, 1925	"
"	6.5	"	"	"	found in preliminary examination	"	"	"	"	"
"		"	"	"	few root hairs; endotroph in	"	"	"	"	"
"		"	"	"	thickened root tips	"	"	"	"	21,
<i>Viola sororia</i>	6.6	oak-hickory forest		"	endotroph in roots above nodules;	"	"	"	Johnson Apr. 19, 1925	"
"		"	"	"	forming vesicles	"	"	"	"	"
<i>Fraxinus pennsylvanica</i>	6.8	"	"	"	few root hairs; tips of roots	"	"	"	"	"
var. <i>lanceolata</i>		"	"	"	darkened	"	"	"	"	"
<i>Galium aparine</i>	6.2	"	"	"	root hairs sparse; distorted;	"	"	"	"	"
"		"	"	"	tips of roots swollen; ectotroph	"	"	"	"	"
"		"	"	"	and abundant endotroph of appar-	"	"	"	"	"
"		"	"	"	ently the same fungus	"	"	"	"	"
<i>Galium triflorum</i>	6.3	"	"	"	root hairs present but scarce;	"	"	"	May 20, 1925	"
"		"	"	"	digestion of phycomycetoid endo-	"	"	"	"	"
"		"	"	"	troph; arbuscles present	"	"	"	"	"
"		"	"	"	same as above; more arbuscle	"	"	"	May 20, 1925	"
"		"	"	"	formation	"	"	"	"	"

TABLE II
PLANTS IN WHICH MYCORRHIZA WERE FOUND BUT NOT ON EVERY EXAMINATION

Species	pH of soil solution	Habitat of higher plant	Fungus Pres. Abs.	Important characters of higher plant or fungus	Place of collection (county)	Date of Collection
<i>Adiantum pedatum</i>	6.9	oak-hickory forest	X	ectotroph; basidiomycete hyphae	Johnson	Apr. 19, 1925
"	5.4	"	X	endotroph; vesicles; root hairs	"	May 20, 1925
"	7.0	"	X	root hairs abundant	"	Oct. 10, 1925
"	6.8	"	X	mycelium abundant in soil about root hairs, but no connection with root noticed	"	"
<i>Cystopteris fragilis</i>	6.7	"	X	roots well developed; root hairs abundant	"	Apr. 19, 1925
"	5.2	"	X	root hairs present; disorganizing endotroph in outer cortical cells of root tip	"	May 20, 1925
<i>Osmunda claytoniana</i>	5.1	dense undergrowth				
"	6.2	oak-hickory forest	X	root hairs sparse	"	"
"		"	X	roots normal, cells packed with starch grains	"	"
"	6.8	"	X	no root hairs; disorganizing endotroph in outer cortical cells of root tip	"	Oct. 10, 1925
<i>Arisæma triphyllum</i>	6.7	"		root hairs sparse	"	"
"	5.4	"	X	root hairs few; large phycomycetoid endotroph with numerous arbuscles	"	Apr. 19, 1925
<i>Quercus macrocarpa</i>	7.6	open edge, bur-oak forest	X	ectotroph abundant; roots examined 8-10" below surface; seedling of 3rd year	Dickinson	June 19, 1925
"	8.1	"	X	same fungal cond. seedling, 2nd yr.	"	"
"	7.7	"	X	"	"	"
"	7.5	"	X	"	"	"
"	7.6	"	X	"	"	"
"	6.6	sandy beach; 15' from water line of lake	X	"	"	July 16, 1925
"		"	X	roots normal and root hairs present	"	July 21, 1925

TABLE III
PLANTS IN WHICH MYCORRHIZA WERE NOT FOUND

Species	pH of soil solution	Habitat of higher plant	Important characters of higher plant or fungus	Place of collection (county)	Date of Collection
<i>Aspidium spinulosum</i>	6.5	north ravine in oak-hickory forest	root hairs present	Johnson Apr. 19, 1925	
<i>Equisetum kansanum</i>	alk.	N.E. slope; open prairie	root hairs abundant	Dickinson July 27, 1925	
<i>Smilacina stellata</i>	7.9	east exposure; oak-hornbeam grove	roots normal	" " 10, "	
" "	8.0	east exposure; long lake shore	" "	" "	" "
<i>Polygonatum commutatum</i>	8.2	wooded east exp. long lake shore	root hairs present	" "	" 9, "
" "	8.2	sandy slope east exp. lake shore	" "	" "	" "
" "	7.7	rather open oak-ash peninsula	" "	" "	" 10, "
<i>Trillium grandiflorum</i>	5.4	coppice growth	few root hairs	Johnson May 20, 1925	
<i>Cypripedium pubescens</i>	6.2	dense woods; north of Homestead	root hairs present but much distorted	Iowa " 10, "	
" "	alk.	dense oak forest	roots long, thick, and tortuous; few root hairs	Dickinson July 27, 1925	
<i>Asarum canadense</i>	5.2	north exposure; coppice growth	no root hairs and no trace of fungus found	Johnson May 20, 1925	
<i>Claytonia virginica</i>	6.6	north ravine; oak-hickory forest	root hairs present	Johnson Apr. 19, 1925	
<i>Anemonella thalictroides</i>	6.8	north ravine; oak-hickory forest	root hairs numerous	" " "	" "

(Continued on page 46)

TABLE III (Cont'd.)

Species	pH of soil solution	Habitat of higher plant	Important characters of higher plant or fungus	Place of collection (county)	Date of collection
<i>Dicentra cucullaria</i>	6.6	ravine; oak-hickory forest	root hairs well developed; no trace of fungus in roots or tubers	Johnson	Apr. 19, 1925
<i>Psedera quinquefolia</i>	8.2	sandy slope; east ex- posure; wooded shore line of lake	root hairs present	Dickinson	July 9, 1925
<i>Viola pubescens</i>	7.0	ravine; oak-hickory forest	no root hairs; not distorted	Johnson	Apr. 19, 1925
<i>Viola</i> sp.	6.4	sandy beach; 15' from water line of lake	root hairs abundant; phycomy- coid mycelium about roots in soil	Dickinson	July 21, 1925
" "	6.5	" " " "	same condition as above; no connection with root in either case	" "	" "
<i>Polemonium reptans</i>	6.7	north ravine; oak- hickory forest	roots normal; root hairs present	" "	Apr. 19, 1925
<i>Galium</i> sp.	6.6	" " " "	root hairs well developed	" "	" "

to families, and genera within each family. With each collection is given the hydrogen-ion concentration of the soil solution; the distinctive characters of the root-fungus association, and of the fungus involved; root characters of the higher plant; the habitat of the higher plant; and the place and date of collection.

Table II lists in phylogenetic order those species in which mycorrhiza were found in some but not all specimens examined, giving the number of collections of each; the pH of the soil solution; the habitat of the higher plant; and the place and date of collection. In those cases which revealed mycorrhiza the fungal condition is given.

Table III lists in like manner those species in which no mycorrhizal condition was found giving for each collection the hydrogen-ion concentration of the soil solution; the habitat of the higher plant, and its important characters; and the place and date of collection.

DISCUSSION

The endotroph found in the two examinations of *Melilotus* proved of interest, as mycorrhiza has been reported for the Leguminosæ only since 1923 (Jones, 6). Atkinson (1) reported on a microsymbiont in the root tubercle of *Vicia sativa* in 1893, but did not refer to it as a fungus. His figures of this microsymbiont clearly show it to be similar to the mycorrhizal, phycomycetoid, endotrophic fungi with the arbuscle formations. Jones has found mycorrhiza-like fungi in the roots of fifteen species of Leguminosæ. The fungus is reported as a Phycomycete, occasionally forming vesicles and arbuscles. The roots of *Melilotus* which I examined possessed bacterial nodules, and the fungus endotroph was found in the cortical and epidermal cells some distance above the nodules (figs. 27, 28; pl. 5). No trace of a fungus was found in the hypertrophied cells of the nodules.

The two collections of *Hepatica* were from widely separated localities, one being from a ravine in a dense woods, and the other from a north-exposed, limestone cliff. The branching, phycomycetoid, endotroph found in both was apparently the same fungus, found always in roots that were distorted and wanting in root hairs. No trace of a fungus was found more than 1 cm. from the root tip (figs. 24, 25; pl. 5). On the same plants no trace of a fungus was

found in those roots which possessed root hairs and appeared normal.

The fungus found in *Orchis* (fig. 18; pl. 4), and in *Corallorrhiza* (pl. 3) appeared to be the typical orchid fungus as described by Knudson (7). This was very abundant in the subterranean parts of *Corallorrhiza* in various stages of infection by the fungus, and of digestion of the fungus by the host. The two collections of *Orchis* were from different localities, one being from a group of plants in a rather dense woods, and the other being a lone specimen from an open coppice growth. Both specimens possessed good root hair development, and the fungus of the former was confined to but two cortical cells in one root (of the six roots examined), while the latter showed abundant endotrophic hyphæ about 2 cm. from the tips of the roots. The first was collected April 19, and the second May 20. In considering the data of Table I it is seen that more than one-third of the collections were made in April, but of those species collected in both April and May, and in collections made in May alone, the development of the root fungus was usually better in the later collections.

The two collections of *Podophyllum* made in April revealed a late state in the fungus infection (figs. 42, 43; pl. 7). Most of the roots possessed an endotroph in the shape of a small branched, phycomycetoid fungus, mostly in the inner cortical cells near the endodermis. The cells near the endodermis showed stages of disorganization and digestion of the fungus with the appearance of starch grains. Normal cells were filled with starch grains. The fungus occurred as far back as 2 cm. from the root tip. Root hairs were present in both collections.

It is also to be noticed in the first table that the mycorrhiza of the ferns and herbaceous plants are endotrophic in habit, with the exception of *Sanguinaria*, *Onoclea* and one collection of *Pteris*. In examining such plants in the field it is often difficult to determine whether or not there is a fungus association present, and it is usually necessary to examine the roots microscopically before one can be certain. In the endotrophic association there are in most cases a few root hairs present on the roots, although they may be greatly twisted and distorted, but in some, as in the case of *Podophyllum* discussed previously, the root hair development may appear to be quite normal. The roots of *Caulophyllum* were extremely interesting, being massed into a great tangle, all eight to ten inches long,

seldom branched, spirally twisted, and of the same diameter throughout, except for a slight swelling at the tip. There was no sign of root hair formation. On examination of freehand sections, the root tips were found to be filled with a large, phycomycetoid endotroph. The hyphæ were seen to enter between epidermal cells, the growth being both intercellular, and intracellular.

Of the ferns possessing mycorrhiza, all revealed an endotrophic fungus except *Onoclea*, and one collection of *Pteris*. The ectotroph of *Onoclea sensibilis* appeared to be the same as that of the hornbeam and oak. The ectotroph of *Pteris*, however, was composed of very small, branching hyphæ. The weft was of considerable thickness near the root tip, and at places on the older roots (fig. 11; pl. 2). One collection of *Pteris* possessed an enormous endotroph forming arbuscles (fig. 10; pl. 2), in addition to the ectotroph. These were apparently different fungi. The latter collection, as can be noticed in the table, came from a forest soil with a pH value of 7.2, whereas the former came from a soil which gave a reaction of pH 6.4. Such results are not in accordance with what some of the literature on this phase of mycorrhiza would lead one to expect. Melin (12) has stated that mycorrhizal fungi thrive best in a soil of pH 5.0 or lower, and that there is poor development in neutral soil. Knudson (7) in studying the germination of orchid seeds, found that best growth of seedlings was obtained in inoculated cultures where the pH value was 0.2 to 4.4. The controls, or uninoculated cultures, remained at pH 5.7. Knudson is of the opinion that in the orchid, at least, the increase in the hydrogen-ion concentration is due to the fungus. The two orchids in which mycorrhiza were found in this investigation were in acid soil, one being in a soil of pH 6.8. But of the thirty-three collections including twenty species of plants listed in Table I, all but nine were in a soil of pH 6.5 or more, ten of them being collected in soils with pH values ranging from 7.0 to 8.0.

Of those species collected in alkaline soils the mycorrhizal fungus was endotrophic in habit except in *Ostrya* and *Pteris*. The ectotrophic weft found in all plants of *Ostrya* that were examined was similar to the weft found in oak and cottonwood (pl. 6). The weft, or fungus mantle, was composed of septate hyphæ, and in several collections masses of loose, basidiomycete mycelium were found in the soil about the root. No clamp-connections were found in the hyphæ of the weft, nor in those collections where the same fungus

was endotrophic as well as ectotrophic. Melin (9) reports in this type of fungus the existence of a pseudoparenchymous mass of hyphæ within the cortical cells, and believes that it is here that infection sets in, the fungus mantle being formed later. In the hornbeam, under the oil immersion lens, I observed the mass of septate haustoria or intercellular hyphal tips about the epidermal cells and penetrating between the cortical cells, but I saw no instance in which they seemed to be intracellular. Five of the young hornbeam plants examined were seedlings of the first year, and two were in their second year of growth. It should be noted in this connection that not only in *Ostrya*, but in *Fraxinus*, and in one collection of *Pteris*, the well developed ectotroph was associated with an endotroph believed to be the same fungus.

The ectotroph of *Populus* seems to be the same fungus as that of *Ostrya*. The cottonwood plants were collected in the sand about fifteen feet from the water line of the lake, where the pH value for all collections was near 6.5. In one collection a phycomycetoid endotroph was present also (figs. 35, 36; pl. 6).

The data of Table II require more discussion. It should be noted that the collections of *Arisæma* and *Cystopteris* are the only collections definitely corroborating previous evidence on mycorrhizal relationship to hydrogen-ion concentration as given by other workers. In the first species the collection which revealed an abundant, phycomycetoid endotroph and the collection which proved to be negative, were made in the same woods, the former in late May, and the latter on April 19. The hydrogen-ion concentrations of the two soils were pH 5.4 and 6.7 respectively. The endotroph of *Arisæma* (fig. 22; pl. 4) exhibited numerous arbuscle formations similar to those described by Demeter (2) and Gallaud (4). Likewise, in the case of the two collections of *Cystopteris*, one possessed a mycorrhizal endotroph, and was collected the same time and place as the positive collection of *Arisæma*. The other, which was negative, was collected with the negative collection of *Arisæma*. The hydrogen-ion concentrations of the two soils were pH 5.2 and 6.7, being practically the same as the values for the two collections of *Arisæma*. It should be noted that both negative collections were made in the middle of April, the positive late in May, and that in the discussion of Table I it was emphasized in connection with *Orchis* that although over one-third of the collections in that table were made

in April, there was in most cases a better mycorrhizal development in those collections made in May.

The third collection of *Osmunda*, and the second collection of *Adiantum*, possessed endotrophic mycorrhiza as did most of the ferns listed in the first table. In the first collection of *Adiantum* an ectotrophic basidiomycete fungus (figs. 1, 2; pl. 1) formed a mantle of considerable thickness. Thus of the eight collections of ferns in which mycorrhizal fungi were found, all possessed an endotrophic fungus except one collection of *Adiantum*, and the collection of *Onoclea*. The two examples cited are in agreement with the findings of others as to the occurrence of mycorrhiza, but it will be noted that in the case of *Adiantum* the positive collection possessing an ectotrophic fungus was from a neutral soil, and the positive collection possessing an endotrophic fungus was from an acid soil, while both negative collections were from nearly neutral soils. However, the two positive collections were made in the spring, and the two negative in October. Also, in the case of *Osmunda*, the negative collections were from soils of pH 5.1 and 6.2, one being made in April and one in October, while the positive collection was from a soil of pH 6.8, collected in October.

The vesicles in the endotroph of *Adiantum* (figs. 3, 5; pl. 1; and fig. 2; pl. 8), were similar to those described by West (24) for the mycorrhiza of the Marattiaceæ, and by Demeter (2), and Magrou (8). Terminal and intercalary vesicles were observed, both occurring intracellularly and intercellularly. There were no root hairs present, and the roots were much distorted, with short thick branches, the tips being black. In examination of prepared slides the extent of cellular disorganization near the endodermis, and the abundance of the large, branched, elongate hyphæ suggest a possible case of true parasitism on the part of the fungus. Since, in external appearance the roots exhibited the usual mycorrhizal characters for the ferns, it seems probable that the mycorrhizal endotroph had overcome the capacity of the roots to hold the fungus in check.

The ectotroph of the bur-oak (figs. 38, 39; pl. 6) appeared identical with that found in the cottonwood and hornbeam, forming a pseudoparenchymous layer about the short, thick, lateral roots. (See fig. 46; pl. 8). The external characters of the roots and the character of the fungus layer forming the mantle were typical of the ectotrophic mycorrhiza of common forest trees, as described by Frank (3) and others. On a lateral root, 0.12 mm. in diameter, the

thickness of the fungus web averaged 20 microns, a condition found in general for all woodland collections of *Quercus*. Six of the collections were made at the edge of a bur-oak forest, some of the seedlings being quite in the open. One of the seedlings examined was in the first year of growth, three were in the second, and one in the third. All were rooted from three to ten inches below the surface of the soil, and none possessed roots with root hairs. The soil was alkaline, the hydrogen-ion concentrations for the soil solutions ranging from pH 7.5 to 8.1, as shown in the table.

One collection of *Quercus*, a seedling of the first year, growing in the sand about fifteen feet from the water of the lake, proved negative. This collection was made at the same time as that of *Populus* which possessed the ectotrophic fungus and the plants were only a few feet apart. The pH value of the soil solution of the sandy beach was 6.6 for both collections. In the oak the lateral roots were normal, root hairs were present in abundance, but distorted due to growth in the sand.

Table III requires little discussion, as negative results contribute no conclusive evidence, especially when so few collections of individual species are recorded. Of the fifteen species in which mycorrhiza were not found there was but one collection each of all but four. On comparing the notes in Tables I and II it will be found that of the thirteen species collected, with two or more collections of each, approximately all but one-third gave positive results for each collection. Thus it is highly probable that at least five of the fifteen species listed in Table III do ordinarily have mycorrhiza. With positive results in *Equisetum arvense*, *Smilacina racemosa*, *Viola sororia*, and two species of *Galium*, mycorrhiza would be expected to be present in the species of the same genera listed in Table III. With so much evidence in the literature regarding the presence of a fungus in the orchids, the negative results in the case of *Cypripedium* were surprising. Root hairs were present in both collections of *Cypripedium*. One collection was made in Iowa County, growing in a fairly acid soil in a dense woods, and flowering; while the other was a lone specimen in a bur-oak woods of Dickinson County, where the soil was alkaline. Likewise, the two collections of *Smilacina stellata* were from the alkaline soil of Dickinson County, whereas the two collections of *S. racemosa* giving positive results were from the more acid soils of Johnson County.

Correlating the data of the three tables in regard to the hydrogen-

ion concentration of the soil solution it is found that for the seventy collections made, fifty-one were from soils of pH 6.5, or more, the highest pH value recorded being 8.2. The value of pH 6.5 is taken as an arbitrary value below which conditions are in general more favorable for the development of soil and root fungi. Melin (12) has investigated the influence of hydrogen-ion concentration of soils and culture media on the vigor of the pine and fir root-fungi. He concludes that in general mycorrhizal fungi thrive best at pH 5.0 or slightly lower, with poor development at pH 7.0; and that *Rhizoctonia sylvestris* and *Mycelium r. atrovirens* thrive equally well in neutral and acid media, the latter thriving in all types of forest soil. In view of these observations it seems probable that the value of pH 6.5 chosen above is too high. The ectotrophic fungus found so commonly in this investigation on *Ostrya* and *Quercus* (and on one collection of *Populus* from the same region), is believed to be a *Rhizoctonia*, and all except the collection of *Populus* were taken from soils with pH values ranging from 7.2 to 8.1.

Of the fifty-one collections taken from soils of pH 6.5 or of a higher pH value, thirty (representing seventeen species) possessed mycorrhiza-like conditions. Seventeen (56 per cent) of the thirty were from soils ranging from 7.0 to 8.1 (representing eight species of plants). Of the remaining nineteen collections of pH value less than 6.5, thirteen (representing the same number of species) were positive. Eight of these (representing eight species) were from soils ranging from pH 4.9 to 5.5. These numbers substantiate to some extent the results of Melin and other workers, as discussed previously, in that approximately 70 per cent of the collections with a pH value below 6.5 were positive, indicating that an acid soil is the more favorable for mycorrhiza; also in that nearly half of the collections from soils of pH 6.5 or of a higher pH value were negative. It is evident that approximately 77 per cent of the negative collections, and 70 per cent of all positive collections were from soils of pH 6.5 or above, but these figures cannot be balanced against the preceding figures, for more than 70 per cent of all collections were made on alkaline, neutral, or slightly acid soils.

Thus, it seems evident that in the Iowa forest flora, mycorrhiza or mycorrhiza-like fungi are of common occurrence, and are widespread among species of higher plants, in acid, neutral, and alkaline soils, but are more common and better developed in soils of pH value below 6.5. Far-fetched generalizations should not be drawn

from too little evidence, but it is believed that the evidence cited in the above discussion concerning mycorrhizal development and hydrogen-ion concentration, is worthy of note in that (1) the pH values are fairly accurate; (2) the species of plants examined are quite representative of the Iowa forest flora; (3) the types of soils from which collections were made are also representative forest soils of Iowa; and (4) collections were made throughout the growing season.

SUMMARY OF RESULTS

(1) The seventy individual plants collected and examined from typical forested areas of Johnson, Iowa, and Dickinson counties represented twenty-one families, thirty-four genera, and forty species.

(2) Sixteen of the collections were of Pteridophytes, representing four families, eight genera, and nine species. All other collections were of higher plants.

(3) Of the total number of collections, forty-three, representing sixteen families, twenty-four genera, and twenty-five species, disclosed association with a mycorrhiza-like fungus.

(4) Of the forty species examined, twenty showed a root-fungus association in every plant examined, five in some cases but not in others, and fifteen showed no trace of mycorrhizal fungi.

(5) Of the forty-three positive collections twenty-four possessed mycorrhizal endotrophs, fifteen mycorrhizal ectotrophs, and four had both endotrophic and ectotrophic root-fungi.

(6) In the collection of *Fraxinus*, one collection of *Ostrya* and one collection of *Pteris*, the endotroph and ectotroph are in each case believed to be the same fungus.

(7) Two of the twenty-four collections with endotrophic fungi showed vesicle formations, one being of *Adiantum pedatum*, and the other of *Melilotus alba*.

(8) The following species with endotrophs showed arbuscule formations: *Arisæma triphyllum*, *Botrychium virginianum*, *Erythronium albidum*, *Galium aparine*, *G. triflorum*, *Pteris aquilina*, *Smilacina racemosa*, and *Uvularia perfoliata*.

(9) The ectotroph of *Ostrya*, *Quercus*, *Populus*, and *Onoclea*, is believed to be the same fungus, probably a *Rhizoctonia*. *Ostrya virginiana* and *Quercus macrocarpa* are provided constantly with a fungus ectotrophic in character.

(10) In ectotrophic forms intercellular hyphæ were observed about the epidermal cells, and between cortical cells, but no intracellular, pseudo-parenchymous masses were found.

(11) In endotrophic forms both intercellular and intracellular hyphæ were observed, the hyphæ passing freely from one cell to another, but most growth being intracellular.

(12) In endotrophic forms hyphæ were observed entering between epidermal cells and penetrating the walls of the cortical cells.

(13) The usual stages of infection and disorganization as reported by other workers were observed in the endotrophic forms.

(14) Fungus hyphæ were found in epidermal cells in several cases but the means of infection could not be determined. They were observed to extend from epidermal cells into cortical cells in *Smilacina racemosa*. They were never found entering the epidermal cells directly as reported by Melin (9) and West (24).

(15) The endotroph of *Orchis*, and of *Corallorrhiza* is believed to be the typical orchid endotroph.

(16) Numerous roots of two collections of *Cypripedium* were examined and no trace of a fungus was found. Both plants were thriving, one being in flower.

(17) The pH value of the soil solutions of plants examined ranged from 4.9 to 8.2. The soils were typical forest soils of Johnson, Iowa, and Dickinson counties.

(18) Fifty-one of the seventy collections were from soils of pH 6.5 or more. Thus more than 70 per cent of all collections were from alkaline, neutral, or slightly acid soil.

(19) Of the forty-three positive collections and twenty-seven negative collections, approximately 70 per cent of the former and 77 per cent of the latter were from soils of pH 6.5 or more.

(20) Of the nineteen collections from soils below 6.5 in pH value, 70 per cent were positive.

CONCLUSIONS

(1) Mycorrhiza-like fungi are of common occurrence in the Iowa forest flora, and are associated with higher plants of wide family relationship.

(2) In general, the endotrophic forms are more common than the ectotrophic in ferns and herbaceous higher plants.

(3) In ectotrophic forms haustoria or intercellular hyphal

branches penetrate between the epidermal cells, and in some cases penetrate between the cortical cells of the root.

(4) A fungus may be either ectotrophic, or endotrophic, or both in habit, in its association with the root of a higher plant.

(5) Mycorrhiza-like fungi occur in Iowa, associated with higher plants in acid, neutral, and alkaline soils, but they are more common and develop better in soils with a pH value below 6.5.

These studies were carried out under the direction of Professor G. W. Martin, to whom I am indebted for helpful suggestions and criticisms, and for the abundant collections of *Corallorrhiza odontorhiza* which was the incentive for this particular study at the State University of Iowa.

BIBLIOGRAPHY

1. Atkinson, G. F. Contribution to the biology of the organism causing leguminous tubercles. Bot. Gaz. 18; 157-166. 1893.
2. Demeter, H. Über "Plasmoptysen-Mykorrhiza." Flora 116; 405-456. 1923.
3. Frank, B. Ueber die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unter-irdische Pilze. Ber. d. deutsch. Bot. Ges. 3: 128-145. 1885.
4. Gallaud, J. Études sur les mycorrhizes endotrophes. Rev. gen. de Bot. 17: 5-48; 66-85; 123-136; 223-239; 313-325; 423-433; 479-500. 1905.
5. Goddard, H. N. Can fungi living in agricultural soil assimilate free nitrogen? Bot. Gaz. 56: 249-304. 1913.
6. Jones, F. R. A mycorrhizal fungus in the roots of legumes and some other plants. Jour. Agr. Res. 29: 459-470. 1924.
7. Knudson, L. Physiological study of the symbiotic germination of orchid seeds. Bot. Gaz. 79: 345-379. 1925.
8. Magrou, J. Symbiosis and tuberization. Ann. Sci. Nat. Bot. 10 Ser., 3: 181-275. 1921.
9. Melin, E. On the mycorrhizas of *Pinus silvestris* and *Picea abies*. Jour. Ecol. 9: 254-257. 1921.
10. ——— Experimentelle Untersuchungen über die Konstitution und Oekologie der Mycorrhizen von *Pinus silvestris* und *Picea abies*. Mykol. Untersuch. und Ber. 2: 73-330. 1923. Abst. from Rev. of Appl. Myc. 3: 540-541. 1924.
11. ——— Experimentelle Untersuchungen über die Birken- und Espenmycorrhizen und ihre Pilzsymbionten. Svensk. Bot. Tidskr. 4: 479-520. 1923. Abst. from Rev. of Appl. Myc. 3: 358-359. 1924.
12. ——— Über den Einfluss der Wasserstoffionkonzentrationen auf die Virulenz der Wurzelpilze von Kiefer und Fichte. Bot. Notiser. 1: 38-48. 1924. Abst. from Rev. of Appl. Myc. 3: 470. 1924.
13. ——— and Helleberg, K. Über die Aktivität von proteolytischen und verwandten Enzymen einiger als Mycorrhizenpilze bekannten Hymenomyceten. Biochem. Zeitschr. 157: 146-155. 1925.
14. Miehle, H. Anatomische Untersuchungen der Pilzsymbiose bei *Casuarina equisetifolia* nebst einigen Bemerkungen über das Mykorrhizenproblem. Flora: 111-112: 431-449. 1918.
15. Molisch, H. Pflanzenphysiologie. 1917.
16. Paulson, R. Tree Mycorrhiza. Trans. Brit. Myc. Soc. 9: 213-217. 1924.
17. Peyronel, B. Fructification de l'endophyte à arbuscules et à vésicules des mycorrhizes endotrophes. Bull. Soc. Myc. de France 39: 119-126. 1923.
18. Rayner, M. C. Obligate symbiosis in *Calluna vulgaris*. Ann. Bot. 29: 97-135. 1915.

19. ——— The nutrition of mycorrhiza plants; *Calluna vulgaris*. Brit. Jour. Exp. Biol. 2: 265-293. 1925. Abst. from Rev. Appl. Myc. 4: 428-430. 1925.
20. ——— An endotrophic fungus in the Coniferae. Nature 115: 14-15. 1925.
21. ——— Mycorrhiza. New Phytol. 25: 1-50. 1926. (To be continued).
22. Skene, M. The Biology of Flowering Plants. London, 1924.
23. Thomas, M. B. The genus *Corallorrhiza*. Bot. Gaz. 18: 166-170. 1893.
24. West, C. On *Stigeosporium marattiacearum* and the mycorrhiza of the Marattiaceae. Ann. Bot. 31: 77-99. 1917.

PLATES

All drawings were made with the aid of camera lucida, at a magnification of 630 diameters unless otherwise stated, and reduced one-half in reproduction.

Abbreviations used in labeling

ep—epidermis

en—endodermis

ec—epidermal cell

cc—cortical cell

st—stele

cn—cell nucleus

rc—root cap

fw—fungus web

ctx—cortex

PLATE I

- Fig. 1. Longitudinal section of lateral root of *Adiantum pedatum* showing pseudoparenchymous layer formed by ectotrophic hyphæ.
- Fig. 2. Epidermal cells in longitudinal section near tip of root of same plant. The septate hyphæ of the fungus ectotroph show a clamp connection.
- Fig. 3. Longitudinal section of root of another plant of same species showing intercalary, intracellular vesicle about 8 mm. from tip of root.
- Fig. 4. Longitudinal section of same root showing hyphal branch entering the root between epidermal cells.
- Fig. 5. Cortical cells of same root in longitudinal section showing hyphal growth from one cell to another, but most growth being intracellular. Also a terminal, intracellular vesicle in second layer of cortical cells beneath the epidermis, about 1 cm. from root tip.
- Fig. 6. Longitudinal section of same root showing septate hyphæ of an endotrophic fungus associated with the one forming vesicles, but probably another fungus.
- Fig. 7. Longitudinal section of root of *Botrychium virginianum* showing disorganizing hyphæ of fungus endotroph, and unorganized cell contents, in third and fourth layer of cortical cells beneath the epidermis, about 5 mm. from tip of root.
- Fig. 8. Root of *Equisetum arvense* in longitudinal section showing hyphal characters of fungus in middle cortical cells.

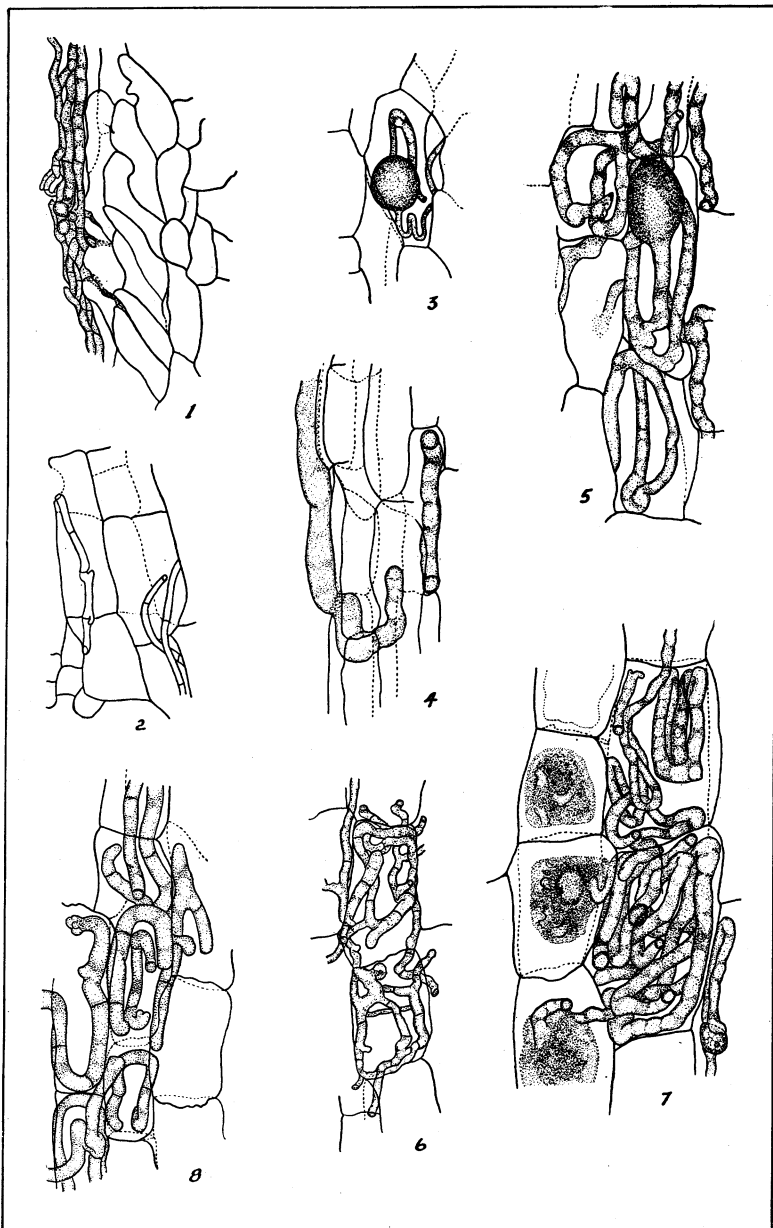


PLATE II

- Fig. 9. Longitudinal section of same root of *Equisetum arvense* showing external epidermal surface and cortical cells beneath, with fungus hyphæ entering between epidermal cells. The flattened tips of the intercellular hyphal branches are pressed against the walls of the first layer of cortical cells beneath.
- Fig. 10. Root of *Pteris aquilina* in longitudinal section showing arbusele formations in large cortical cells, and hyphæ of an ectotrophic fungus of different character; *ep*, epidermis, and *en*, endodermis.
- Fig. 11. Longitudinal section of another part of same root showing hyphæ of fungus ectotroph of fig. 10 entering between two epidermal cells, *ec*, with their intercellular tips pressed against lower surface of large cortical cells, *cc*. Oil immersion; original magnification approximately x 1400.
- Fig. 12. Longitudinal section of root of *Onoclea sensibilis* showing thick weft of ectotrophic hyphæ forming pseudoparenchymous outer layer, and the haustoria penetrating between epidermal cells.
- Fig. 13. Diagram of portion of median longitudinal section of same root tip showing relative thickness of fungus weft to other parts of root. Note the haustoria between the epidermal cells; *en*, endodermis, and *st*, stele.

PLATE II

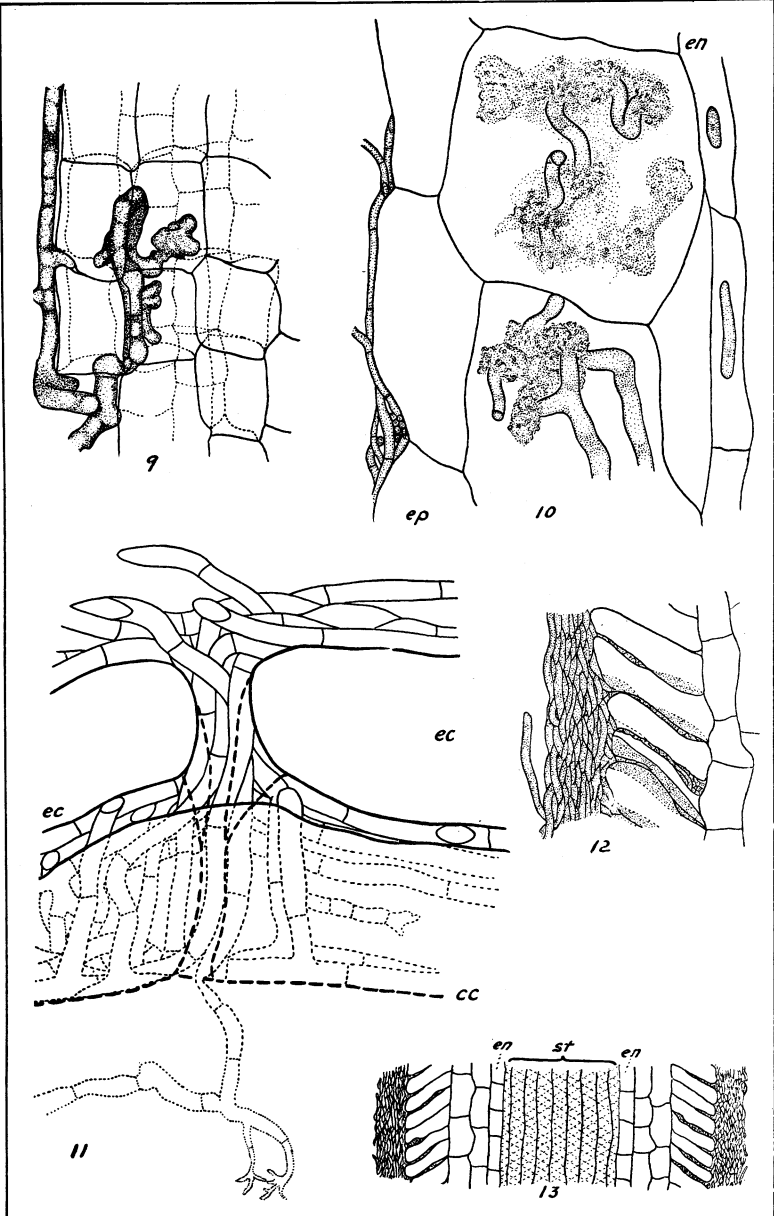


PLATE III

- Fig. 14. *Corallorrhiza odontorhiza*. Longitudinal section of slender, root-like, subterranean part showing hyphæ of typical orchid endotroph in cortical cells immediately beneath the epidermis, *ep*, 1 mm. from tip of "root"; *cn*, cell nucleus.
- Fig. 15. Cross section of similar part ("root") of same plant showing disorganization of fungus hyphæ, in inner cortical cells 4 mm. from the tip. Note enlargement of cell nucleus *cn*, on infection of cell by the fungus.
- Fig. 16. Cross section of short, thick, tuberous, subterranean part of same plant showing fungus hyphæ in epidermal cells.
- Fig. 17. Longitudinal section of similar part showing stages of mycelial disorganization in inner cortical cells.

PLATE III

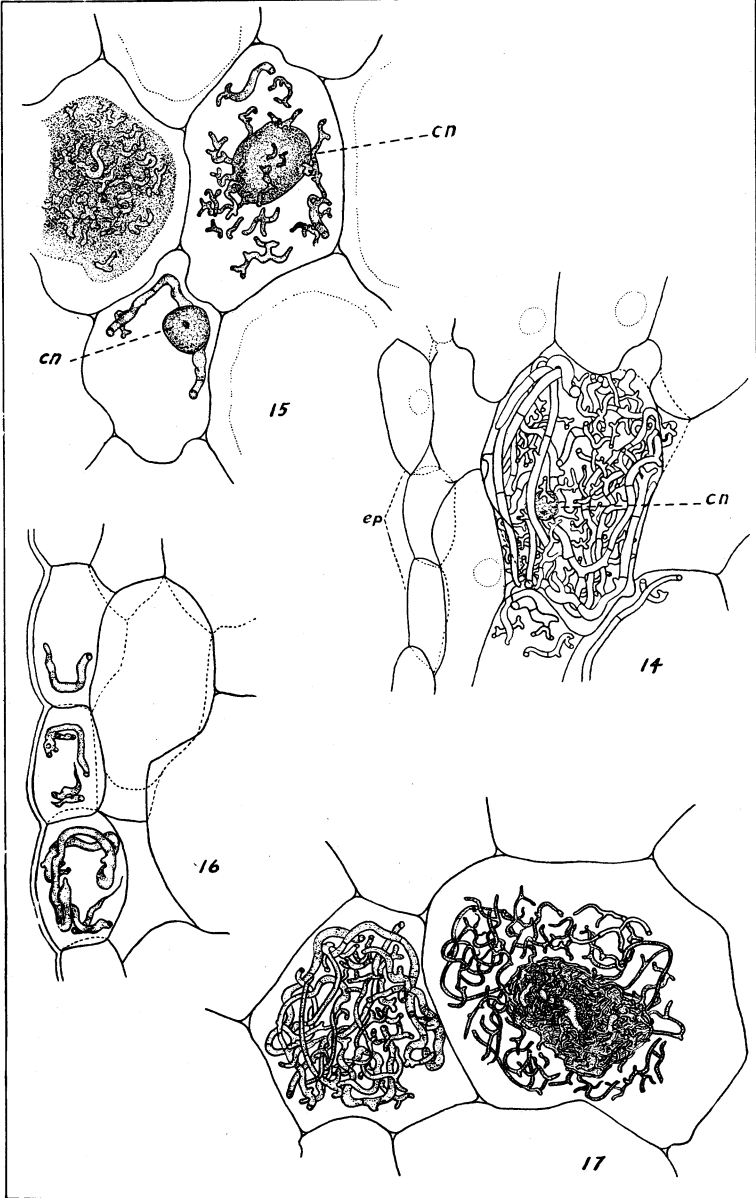


PLATE IV

- Fig. 18. *Orchis spectabilis*. Cross section of root showing typical orchid fungus in cortical cells, and enlargement of cell nucleus *cn*, on infection of cell by fungus.
- Fig. 19. Longitudinal section of root of *Caulophyllum thalictroides* showing phycomycetoid endotroph with branching hyphæ, in inner cortical cells. The normal cell on left shows starch grains, and cell above shows disorganization of hyphæ; *cn*, cell nucleus.
- Fig. 20. Cross section of another root of same plant showing disorganization of hyphæ in an inner cortical cell. The cells are of the third and fourth row beneath the epidermis about 4 mm. from root tip; *cn*, cell nucleus.
- Fig. 21. *Erythronium albidum*. Cross section of root showing hyphæ of the endotroph in second and third layers of cortical cells beneath epidermis.
- Fig. 22. *Arisæma triphyllum*. Longitudinal section of root showing endotroph forming arbuseles in third layer of cortical cells beneath epidermis about 2 cm. from root tip; *cn*, cell nucleus.

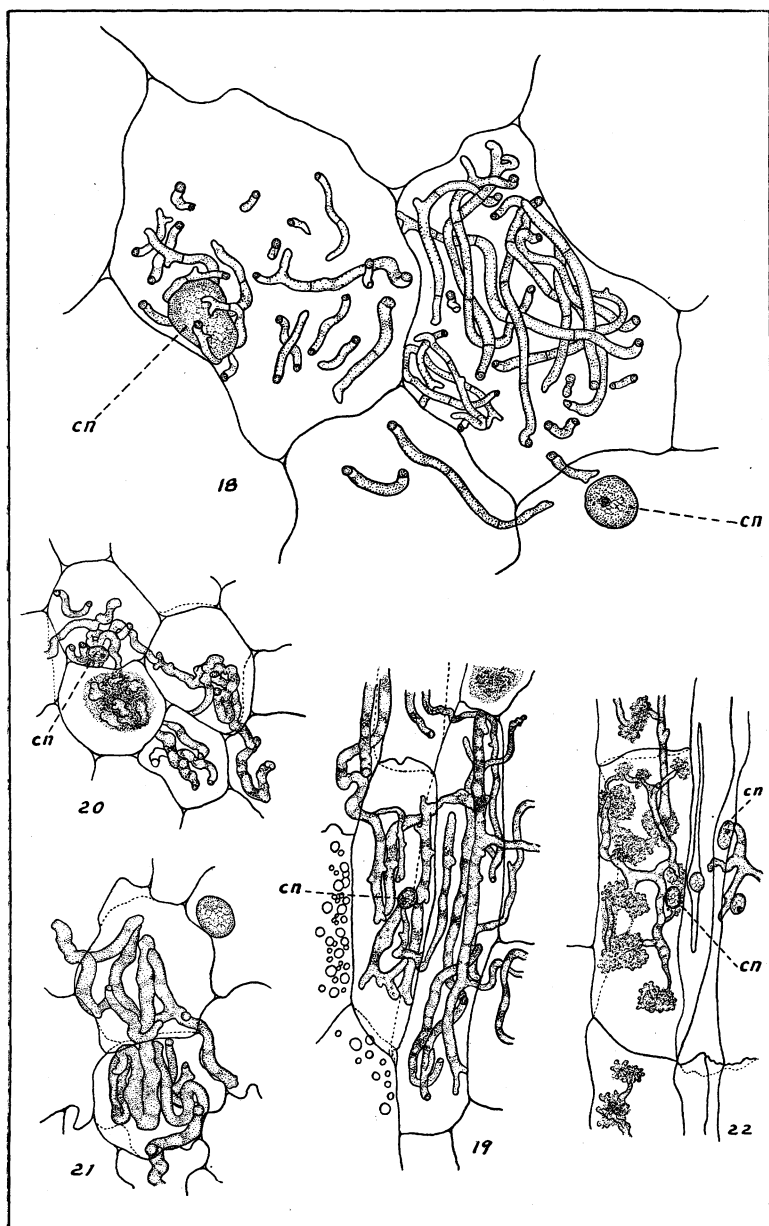


PLATE V

- Fig. 23. *Erythronium albidum*. Longitudinal section of root showing branching hyphæ of fungus endotroph and formation of arbuscles in second and third layers of cortical cells 3 mm. from tip of root.
- Fig. 24. Longitudinal section of root of *Hepatica acutiloba* showing in cortical cells the hyphæ of the endotroph 3 mm. from tip of root.
- Fig. 25. Cross section of root of same plant 2 mm. from tip showing fungus hyphæ and hyphæ being digested; *en*, endodermis; *st*, stele; and *ep*, epidermis.
- Fig. 26. *Melilotus alba*. Cross section of root showing disorganizing phycomycetoid hyphæ in cortical cells.
- Fig. 27. Longitudinal section of root of another plant of same species, through older part of root above bacterial nodules, showing terminal intercellular vesicles between cortical cells.
- Fig. 28. Longitudinal section of same root showing intracellular and intercellular hyphæ near endodermis *en*; *ep*, epidermis.

PLATE V

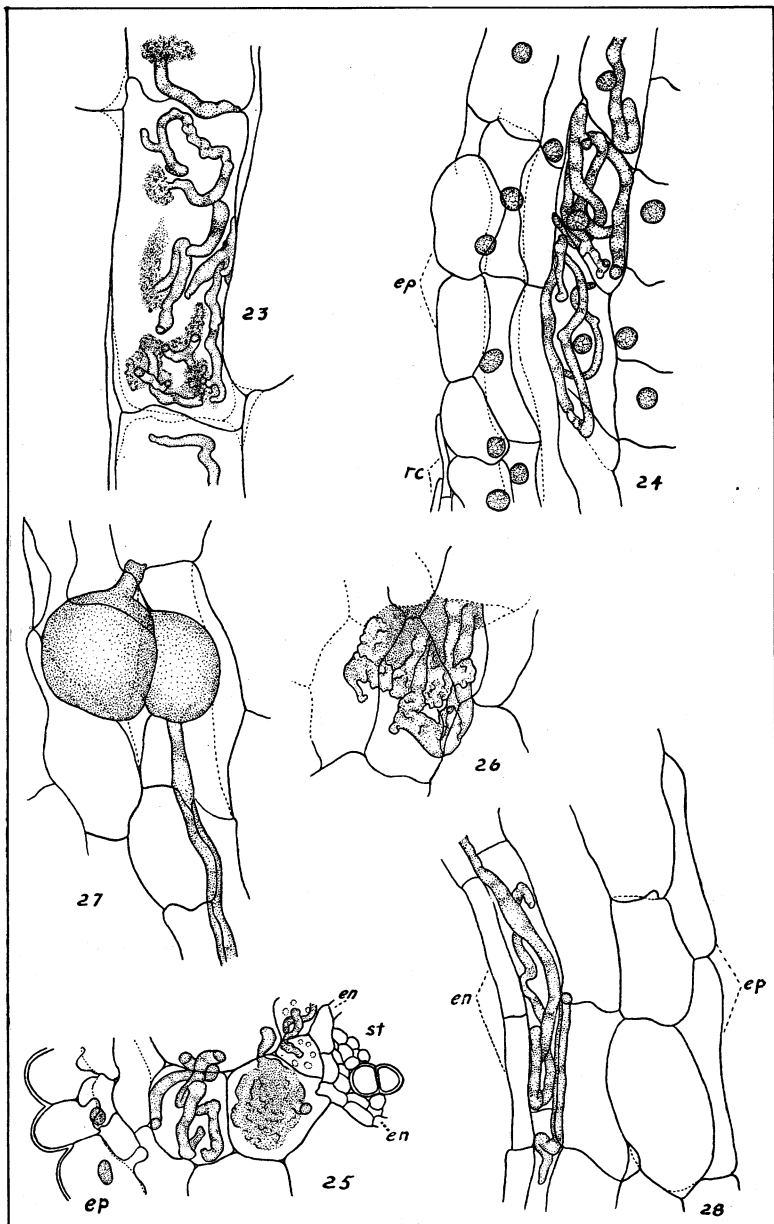


PLATE VI

- Fig. 29. *Ostrya virginiana*. Cross section of short, thick, lateral root, showing outer pseudoparenchymous layer formed by the weft of fungus hyphæ.
- Fig. 30. Longitudinal section of root of same plant showing on external epidermal surface the type of fungus hyphæ which forms the weft in fig. 29.
- Fig. 31. External surface view of hyphæ forming weft on roots of *Ostrya*.
- Fig. 32. Cells in longitudinal section of *Ostrya* root showing hyphæ of ectotroph and haustoria between epidermal cells. Oil immersion; original magnification approximately x 1400.
- Fig. 33. Hyphal character of fungus forming weft in fig. 32.
- Fig. 34. Longitudinal section of *Ostrya* root some distance from tip showing same fungus as an ectotroph and an endotroph; *ep*, epidermis.
- Fig. 35. *Populus deltoides*. Cross section of short lateral root showing pseudoparenchymous layer of hyphæ of fungus ectotroph; *en*, endodermis.
- Fig. 36. Longitudinal section of root of another cottonwood seedling showing endotroph in cells next to endodermis *en*. This condition present mostly some distance from root tip. The ectotroph of fig. 35 was also present on this root at tip.
- Fig. 37. *Fraxinus pennsylvanica* var. *lanceolata*. Longitudinal section of lateral root showing endotrophic hyphæ in cortical cells near root tip.
- Fig. 38. Longitudinal section of root tip of *Quercus macrocarpa* showing ectotrophic fungus hyphæ. Note resemblance to same condition in *Ostrya* (fig. 29), *Populus* (fig. 35), and *Onoclea* (figs. 12 and 13).
- Fig. 39. Diagram of median longitudinal section of same root tip to illustrate relative thickness of fungus weft to other parts of root. Root 0.12 mm. in diameter; average thickness of fungus weft 20 microns; *st*, stele; *ctx*, cortex; and *fw*, fungus weft. (Outlined with camera lucida, l.p.—original magnification approximately x 125.)

PLATE VI

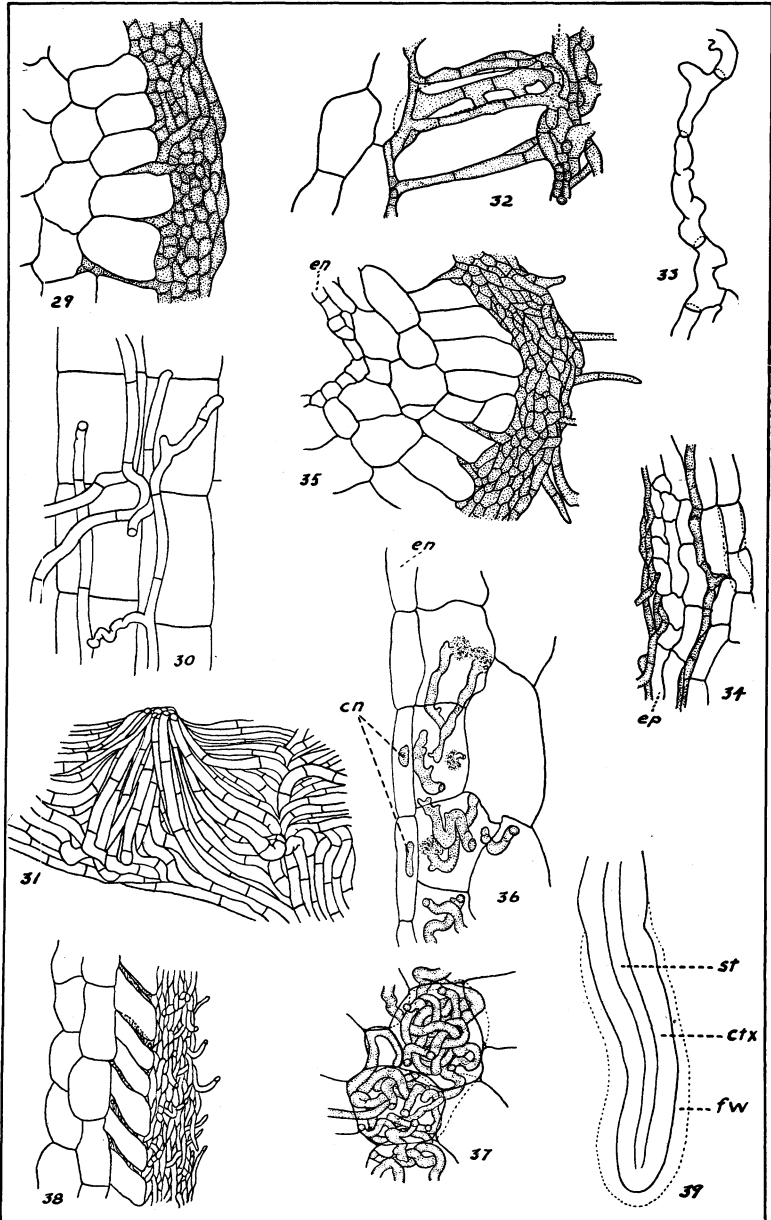


PLATE VII

- Fig. 40. *Uvularia perfoliata*. Middle cortical cells near root tip in longitudinal section showing hyphal characters of endotroph with several arbuscles; *cn*, cell nucleus.
- Fig. 41. *Smilacina racemosa*. Longitudinal section showing hyphæ forming arbuscles in inner cortical cells about 1 cm. from root tip. Hyphæ present in epidermal cell and hyphal branches have entered two cortical cells within. External hyphæ of same character are pressed against the epidermal cells, *ep*. Root hairs were present on this root; *rh*, base of root hair; *cn*, cell nucleus.
- Fig. 42. *Podophyllum peltatum*. Semi-diagrammatic drawing of cross section of root about 1 cm. from tip with shaded cells to show region and relative abundance of fungus endotroph. (Outlined with camera lucida l.p. Original magnification approximately x 125.)
- Fig. 43. Longitudinal section of another root of same plant showing hyphæ and digestion of hyphæ in cortical cells 1 to 2 cm. from root tip. Note starch grains in normal cell below, and in cells showing hyphal digestion; *cn*, cell nucleus.

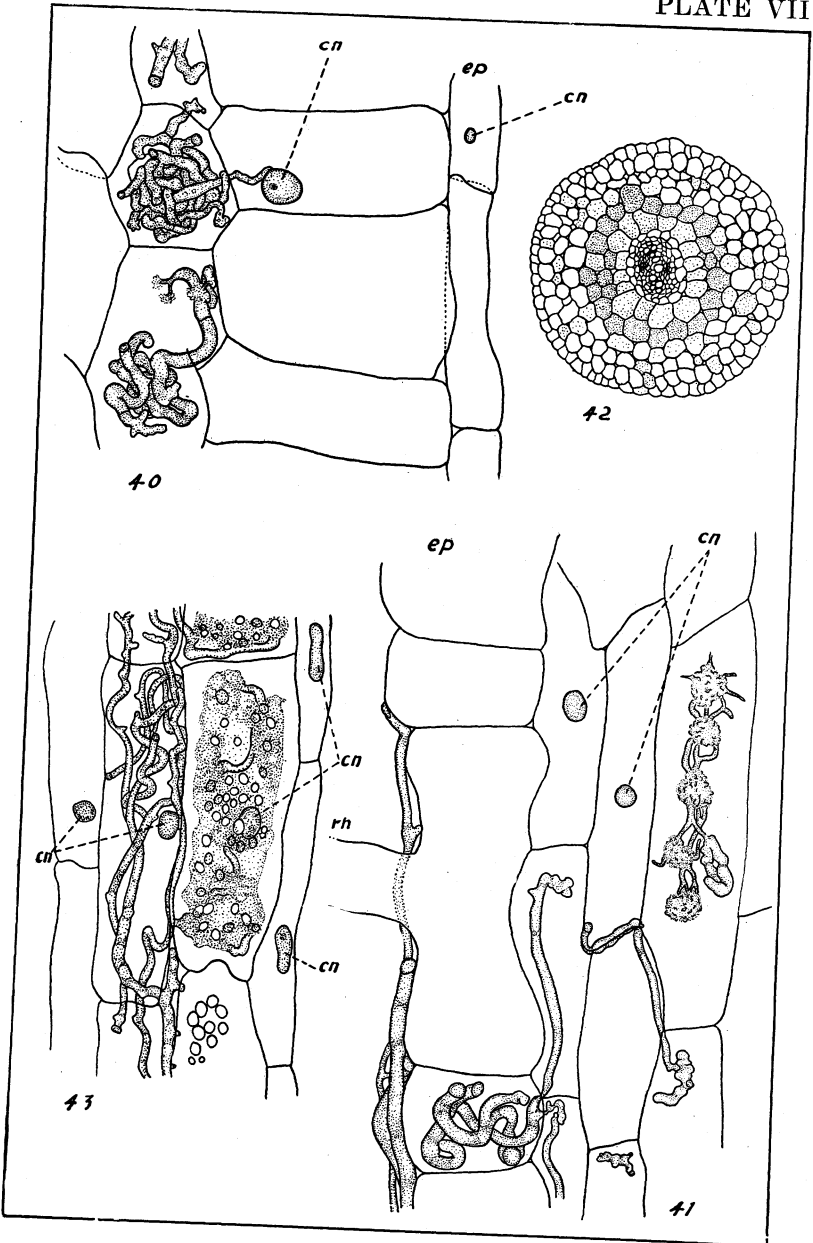
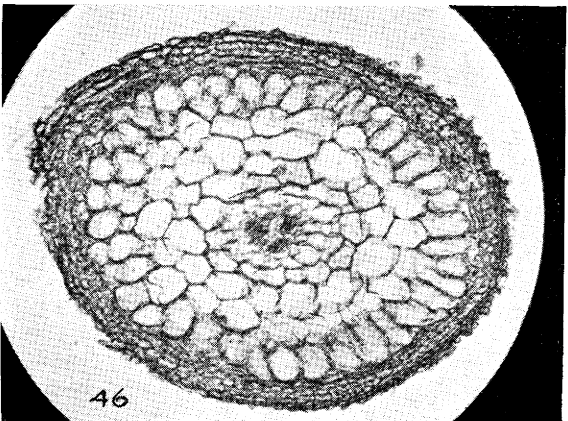
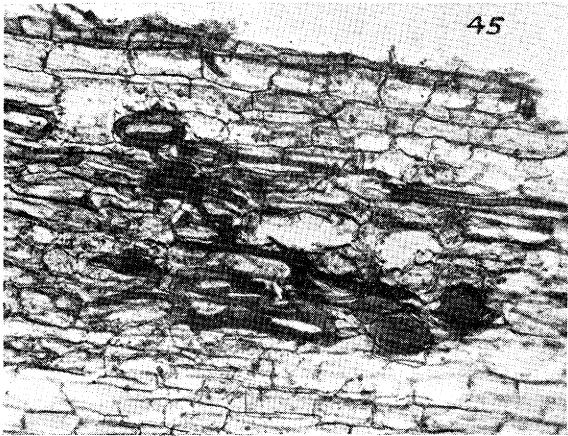
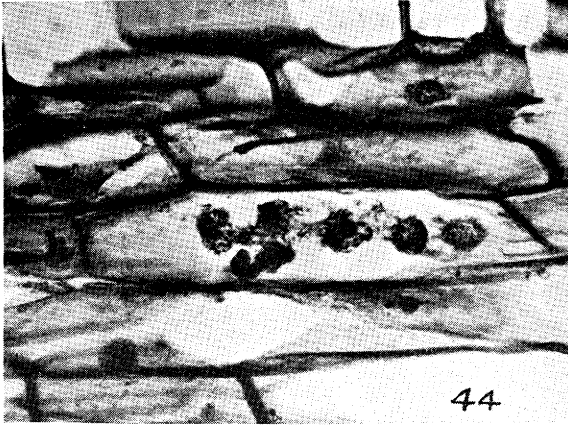


PLATE VIII

- Fig. 44. *Smilacina racemosa*; photomicrograph of longitudinal section showing arbuscule formation in inner cortical cells about 1 cm. from tip of root. (See pl. 7, fig. 41).
- Fig. 45. *Adiantum pedatum*; photomicrograph of longitudinal section showing vesicle formation by fungus endotroph about 1 cm. from tip of root. (See pl. 1).
- Fig. 46. *Quercus macrocarpa*; photomicrograph of cross section of short lateral root showing weft of ectotrophic fungus hyphae forming a pseudoparenchymous-like layer. (See pl. 6, figs. 38 and 39).

PLATE VIII



UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

VOLUME XI

NUMBER 11

METHODS OF MECHANICAL ANALYSIS OF SEDIMENTS

by

CHESTER K. WENTWORTH

PUBLISHED BY THE UNIVERSITY OF IOWA, IOWA CITY, IOWA

METHODS OF MECHANICAL ANALYSIS OF SEDIMENTS

INTRODUCTION

PURPOSE OF MECHANICAL ANALYSIS

The mechanical analysis of a sediment or of any detrital material may serve a number of useful ends. The most obvious result of such analysis is the determination of the several sizes of particles which are present, and from these data the average size and the range of coarseness are at once apparent. A complete mechanical analysis, however, involves not only the determination of the sizes of particles which are present but also the proportions by weight or volume in which the several grades occur. And finally, as the third aim of mechanical analysis, there result the several grades of material, each separated from coarser and finer material and best adapted for study and preservation.

Knowledge of the sizes of particles which are present in a given sediment or artificial material is valuable in a number of ways. In the case of a natural sediment it may determine the name by which the geologist designates the material.¹ In cases where only rough conformability to specifications is required the knowledge of grades present in part determine suitability of the material for various technical uses such as the value of gravel for road metal, sand for glass manufacture, or the finer natural abrasive materials for their several uses. A determination of the several grades present is a means of checking the performance of crushers and separators used in various metallurgical and other commercial mineral operations and the suitability of the materials so prepared for the next stage in the process.

Commonly the proportions of the several grades are determined and these additional data serve much more refined purposes. Thus the geologist is enabled in many instances to deduce the mode of origin and the agent of deposition from a series of mechanical analyses of a certain type of sediment and in cases where this is not possible the data thus derived still serve in a valuable supplementary

¹ Wentworth, C. K., A Scale of Grade and Class Terms for Clastic Sediments, *Journal of Geology*, Vol. XXX, pp. 377-392, 1922.

way.² In other cases mechanical composition may serve as a means of correlating detrital formations in which fossils are missing or rare.³ An increasing use is being made of mechanical analysis as a criterion of suitability of sediments for various commercial and engineering operations. Mechanical composition largely determines the value of materials used for filtering on a large scale, for the construction of earthwork dams and, to a lesser but still important extent, of materials used in concrete construction and of molding sand.⁴ Likewise an increasing attention is being paid to mechanical composition as an important characteristic in writing standard specifications for both natural and artificial materials furnished on contract.

The value of mechanical separation into grades can hardly be overestimated either for critical study or for display and preservation. To the student investigating the petrology or mineralogy of sediments, well cleaned and graded materials are studied with an interest and an economy of time which is impossible with the natural material. For example, in the determination of minerals it is found that the bulk of the minerals of a certain sort or present in a certain form are found in a few grades only. The specialties in the several grades may thus be dealt with in the place where they are most important and where their relations are most clearly seen. There is an economy of attention and a proper perspective and basis for comparison when one is working with materials of similar sizes that is lacking when working with unsorted materials. This principle governs the plan of work in various industrial operations and explains the difficulty one experiences in turning suddenly from very coarse to very fine work of any sort. The desirability of grading materials by size has likewise been recognized by biologists in studying small shells and similar organic objects.

In similar fashion the display of sediments or other such materials is much more effective after grading and especially if the several grades present are displayed in proper order and proportion so as to give a vivid notion of the composition of the natural material.

² Dake, C. L., Missouri School of Mines, Bulletin, Vol. 6, No. 1, p. 152, et seq., 1921.

³ Trowbridge, A. C., and Mortimore, M. E., Correlation of Oil Sands by Sedimentary Analysis, Economic Geology, Vol. XX, pp. 409-423, 1925.

⁴ Littlefield, Max, Natural-bonded Molding Sand Resources of Illinois, Bull. Ills. Geol. Surv., No. 50, 1925.

THE METHODS IN USE

Two principal methods of mechanical analysis are in common use, screening and elutriation. Under elutriation is included the method of settling in still water, though some writers restrict the term to the rising current process of hydraulic classification.⁵ A third method—that of counting—with several variations, completes the list of methods of mechanical analysis. It is unfortunate that a single rapid, accurate and convenient method is not available for the mechanical analysis of materials of all the degrees of coarseness which are common in natural sediments. Many of the natural sediments are of aqueous origin. Such sorting as these exhibit is the result of more or less perfect hydraulic classification in which density, size, shape and surface texture are factors. Because of this fact it has been pointed out that analysis by elutriation is the only satisfactory method of securing a separation which depends on these same factors and thus approaches closely the conditions under which the sediment was deposited. For the finer sediments the method of elutriation in one form or another is admirable, but practical difficulties arise in applying it to materials coarser than the sand grades.⁶ For example, the settling velocity in water for a quartz pebble 5 cm. in diameter is about 5 meters per second. The separation of materials settling at rates of 5 meters per second in still water would involve prohibitive quantities of water and sizes of containers. Likewise the rising current separation of such grades is impracticable. In a tube of 30 centimeters diameter a velocity of 5 meters per second will discharge approximately 5700 gallons of water per minute. It is apparent that some other method for the separation of the coarser grades must be adopted. The use of sieves has been the most common expedient. Because of the cheapness and convenience of manufacture in a wide range of size of opening, woven wire sieves with square openings are the most practical. In using these the constituent particles are classified by cross-sectional size only; the density does not enter as a factor in separations and the shape only as it affects the size of the minimum square through which the rock fragments will pass. Thus in the same grade are found great variation in density, in volume, and in shape and the grade may consist of particles which will not exhibit similar behavior in streams or on beaches under natural conditions. It ap-

⁵ Webster's International Dictionary.

⁶ Holmes, A., *Petrographic Methods and Calculations*, p. 204, London, 1921.

pears to the writer that a separation on the basis of weight of the individual particles would come somewhat closer to the natural hydraulic classification and he has used this method of grading in connection with experiments in pebble abrasion but so far as is known this method has not been used for analysis and automatic methods for such weight separation have not been devised. In spite of its undesirable features the method of sifting in woven wire sieves, by virtue of its convenience, speed and relative accuracy, has come to be the standard method of analysis for the sands and coarser materials. For materials finer than about $1/4$ mm. diameter sieves are less satisfactory because of the tendency of the finer materials to form aggregates and to lodge in the sieve openings. Wire cloth has been woven with openings somewhat smaller than $1/20$ mm. but the finest mesh which proves practicable in the grade scale advocated by the writer is that with $1/16$ mm. openings. This is the lower limit of the method of sifting and for finer grades elutriation or microscopic counting must be used.⁷ The practical upper limit of elutriation may be set at one millimeter. Sediments containing grades from one millimeter downward may be handled wholly by elutriation; those of coarseness ranging from $1/16$ mm. upward may be handled wholly by the method of sifting. It is apparent that many sediments cannot be analysed completely by either method alone. The need for a change from one method to another in the course of the analysis of these sediments is perhaps the most troublesome element in the whole field of mechanical analysis. If the sediment in question is composed wholly of particles of the same density and shape the problem of connecting the hydraulic grade scale with the cross-section grade scale at the point of change involves accurate determination of the hydraulic values of the particles at the lower limit of the smallest sieve grade. If it is desired to use a uniform notation throughout the analysis it is further necessary to determine either (1) hydraulic values of the several critical sieve sizes above the point of change in case a hydraulic notation is to be used, or (2) the cross-section values of the several critical hydraulic values in case the size notation is preferred. When the sediment which is to be analysed contains particles of various densities and shapes, the problem becomes not only much more complicated but is not capable of exact solution and the two types of grade scale must be joined by compromise, giving the larger weight to the shapes and densities

⁷ Holmes, A., *Op. cit.*, p. 204.

which are present in the greatest abundance. Inadequate appreciation of the nature of the problem on the part of students of sediments in the past and the great difficulty of reaching even an approximate solution under standardized conditions has led to much confusion in this field and to the publication of many different combinations of grade scales and to great diversity of assumptions or determined values in connecting the hydraulic and cross-section scales.

This situation seems to have been the principal factor in the decision of certain investigators, notably Udden,⁸ to extend the sieve scale downward by microscopic counting. This method, though to a less degree than that of elutriation, differs from the sieve method and must likewise result in certain discontinuity at the point of change to it from the sieve method. The method of counting, megascopic and microscopic, is applicable to the whole grade range of natural sediments and is undoubtedly in the case of a single critical sample the best method of making an accurate mechanical analysis now available, since by identifying the various constituents the density factors may be taken into account and the resulting analysis suffers from no very serious discontinuity if care is taken to use comparable methods in the megascopic and microscopic portions. Until more exhaustive investigations have been made of the effect of shape on rates of settling, this factor introduces unknown errors in the recognition of the natural hydraulic grades by the method of counting. Furthermore, counting is at best a very laborious procedure and is therefore hardly applicable to large numbers of samples. At the present stage of interpretation of mechanical analysis it appears to be more profitable to examine larger numbers of samples with considerably less theoretical accuracy by some reasonably expeditious method.

SCOPE OF PRESENT PAPER

In the early stages of any sort of investigation great diversity of methods results from the more or less independent work of different pioneer students. This is a most desirable condition for it results in the testing of many different types of procedure and in the exploration of the field of available technique. In later stages, however, the need of comparing results attained by different workers makes

⁸ Udden, J. A., *Mechanical Composition of Clastic Sediments*, Bull. Geol. Soc. Amer., Vol. 25, pp. 655-744, 1914.

some degree of standardization imperative. The great diversity of methods used by pioneer workers is the result in large part of ignorance of methods used by others and of the consequent independent devising of methods.

The purpose of the present paper is to bring together in one place descriptions of some of the more important methods of mechanical analysis where they may guide students of sediments and sedimentation and help to eliminate some of the existing confusion. It is not to be expected that any one method will be used to the entire exclusion of others; this would be an admission that the study of sediments is stagnant or at the limit of growth. But on the other hand, the elimination of the more or less accidental differences of graphic plotting from right to left by some and from left to right by others, and the adoption of some equal ratio geometrical grade scale will be conceded by all as appropriate bases for standardization. In encouraging the adoption of the preferred methods the author has considered it wise to go into considerable detail in the description of the various methods and apparatus, and to supplement the descriptions with diagrammatic illustrations and tabular statements of procedure.

In its inception the present paper was planned as a joint paper by the writer and his colleague, Max S. Littlefield; the latter to prepare the part relating to elutriation, deflocculation and other methods dealing with the finer sediments. As work progressed it became apparent that the technique in this field was so much less well elaborated and, indeed, the purpose and value of mechanical analyses of clay grades so much in question that it was best to complete the present paper with the chief emphasis on the materials coarser than clay and leave the problem of finer materials until further studies make a more authoritative statement possible.

ACKNOWLEDGEMENTS

The author has been assisted from time to time in the testing of methods and apparatus by a number of students who have carried on their work in the Sedimentation Laboratory of the State University of Iowa. Experience in mechanical analysis has been gained as a by-product of other investigations, chief among which have been the studies of Atlantic Coastal Plain terrace gravels for the U. S. Geological Survey by the writer, and studies of Mississippi delta sediments for the War Department by M. S. Littlefield as assistant

to Dr. A. C. Trowbridge. More recently Mr. Littlefield has been engaged in a study of molding sands for the Illinois Geological Survey, in the course of which he has gained much experience in methods of analyses and sampling. To him and to a number of other graduate students at the University of Iowa the writer gratefully acknowledges his indebtedness for suggestions and criticism. For general encouragement and critical discussion of methods and purposes of the study of sediments during the course of studies mentioned above, the writer is especially indebted to A. C. Trowbridge, of the State University of Iowa, and to T. W. Vaughan and M. I. Goldman of the U. S. Geological Survey.

COLLECTION OF SAMPLES

SIZE OF SAMPLE

The size of sample to be collected for mechanical analysis depends on a number of considerations. If the sample is for a single analysis of a homogeneous fine grained material and no further examination is to be made, the amount collected may be small. If, on the other hand, the analysis is to be run in duplicate or the sample is of a coarse, heterogeneous material and the separates are to be studied by other methods, the amount must be much greater. If the mechanical composition of a single thin lamina of fine material is to be determined a small sample will be sufficient, and indeed in such a case an attempt to collect a larger sample is likely to result in the inclusion of material not representative of the lamina and to lead to less accurate results in the end. In commercial sampling it is usually desired to know the average composition of a certain deposit and in this case the materials of different beds or of different areas will need to be included in the sample in proportion to the amounts found on the ground in case a single sample only is to be analysed. In sampling a uniform horizontal series of beds which are unconsolidated this is most easily accomplished by cutting down a uniform channel from top to bottom. This results in a large sample. Any sample in which the amount of material is controlled by nonuniformity, either natural or artificial, may, after thorough mixing, be reduced in size by splitting to the limit imposed by the sizes of the largest constituents or by the purposes to which the sample is to be devoted.⁹

The size of sample needed for an accurate mechanical analysis bears a definite relationship to the coarseness of the sediment. In

⁹ Milner, H. B., *Introduction to Sedimentary Petrology*, pp. 15-17, London, 1922.

general it may be stated that the sample should be large enough to include several fragments which fall in the largest grade present in the deposit. Several fragments may be interpreted as a number sufficiently large so that the probability of a serious accidental deviation from the normal number of such fragments in a sample collected by a reliable random method is small. This number depends in turn on the percentage of the whole which is included in the coarse grade and it is not practicable to adopt specific theoretical standards. It is important, however, that the collector appreciate the principle relating the size of sample to the sizes and abundance of the larger constituents. The following table based on a specific number and percentage of coarser fragments indicates in the second column the smallest size of sample demanded to insure satisfactory accuracy in determining the coarse grade. Several practical considerations are of importance. In general it is hardly profitable to collect less than 125 grams, even of a very fine material, if it is readily obtainable from the outcrop. At the other extreme it is rarely practicable for the geologist to collect samples as large as those demanded by the strict requirements of accuracy. Taking these several limitations into account in the light of experience both in collecting and in subsequent analysis, the scale of sizes given in the last column of the following table is presented as a working suggestion.

TABLE OF SUGGESTED MAXIMUM AND MINIMUM WEIGHTS OF SEDIMENT SAMPLES¹⁰

Coarse Grade	Ideal minimum to determine coarse grade.	Ideal maximum for convenient analysis in 6" sieves ¹¹	Suggested amount of collected sample.
128-64 mm.	256 kg.		32 kg.
64-32 "	32 "		16 "
32-16 "	4 "		8 "
16- 8 "	512 grams		4 "
8- 4 "	64 "	1600 grams	2 "
4- 2 "		200 "	1 "
2- 1 "		25 "	500 grams
1-1/2 "		25 "	250 "
1/2-1/4 "		25 "	125 "
1/4-1/8 "		25 "	125 "
1/8-1/16 "		25 "	125 "

¹⁰ The first column gives the large amounts of coarse material demanded for valid determination of coarse grades. The second column indicates the amounts for the finer grades which are best adapted for sifting and weighing. The third column is a practical compromise from the first and second columns with amounts of the finer sediments increased to give additional material for checking or supplementary study.

¹¹ In case the collected sample is larger than the amount needed for analysis,

CONTAINERS

It is important in collecting samples of sediments for mechanical analysis to provide plenty of containers of ample size. All containers should be tight for the material to be collected and should be stout enough to stand much wear and tear. Loss from broken containers is practically always selective and remaining contents will be of little or no value in mechanical analysis. Cloth bags are most satisfactory for collecting dry materials in the field. They are durable and sufficiently tight if made of fine material and a number of them take up little space until they have been filled. Wet materials, and especially the finer clay sediments in which the original colloidal condition is an important characteristic, should be placed at once in air tight, sealed containers which are entirely filled with the sediment and contained water. Square or round glass jars of various sizes with aluminum screw tops may be obtained from dealers in scientific apparatus and are convenient for wet collecting. Ordinary glass fruit jars are nearly as good for the larger samples, somewhat less expensive and more readily obtainable in the field.

As a guide in ordering sample containers the following tables are presented.

TABLE OF CAPACITIES OF CLOTH BAGS

(Allowing length to tie readily at the top.)

Width and length Inches	Width and length Centimeters	Capacity by weight of dry sand
12 by 18	36 by 46	10 kg.
9 by 14	23 by 36	5 "
7 by 9	18 by 23	2 "
5 by 8	13 by 20	1 "
4 by 6	10 by 15	500 gm.
3 by 4½	8 by 11	200 "
2 by 4	5 by 10	100 "

TABLE OF CAPACITIES OF JARS AND TUBES

Type	Height	Outside diameter	Capacity by weight of dry sand.
1 qt. Mason	190 mm.	105 mm.	1400 gm.
1 pt. "	140 "	90 "	700 "
½ pt. jar	110 "	90 "	400 "
16 oz. Screw	150 "	85 "	800 "
8 oz. "	145 "	65 mm. square	400 "
Round bottom			
shell vial	110 "	30 mm.	35 "
"	60 "	12 "	6 "

split it down. In case, when analysing a coarse sample, the fines at any stage amount *in toto* to much more than the suggested maximum for convenient analysis for that grade, the analysis should be broken at that point and the combined and mixed fines split down to suitable amount before proceeding. The limit is not, of course, fixed or arbitrary, but in general amounts greatly in excess of those given should not be passed through the sieves.

NOTATION AND LABELING

Samples should be accurately labelled so as to indicate the exact locality, the field name of the sediment, the beds or part of the outcrop represented, the proper name of the formation, the method of sampling, the date and the name of the collector. The method of recording these data will usually depend on the form of the collectors field notes. The main desiderata are the same as for ordinary field notes; easy cross reference between the samples, the field notebook and the field map; from any one to either of the other two. The writer prefers to place only a number on the sample and to record all other data in the field notebook under the number. After trying a number of schemes for numbering and lettering notes and localities he has adopted the simple plan of numbering his field stations serially in Arabic numbers, starting from 1 at the beginning of each project. This system does not indicate automatically as do some others the map location of the station. It is necessary in using it to make and number the map location and to make such route notes for each day's travel, referring to the maps used, that another person can readily find the stations in turning from the notebook to the map. This slight disadvantage is more than offset by a number of advantages which are especially important when large numbers of samples are collected. In the first place, in the storage of samples and of the separates derived by mechanical analysis the Arabic numerical scheme is the only one which presents an entirely obvious sequence for arrangement. Systems of letters and numbers, map grating systems or page and notebook notations are all more complicated and less obvious and entail much more confusion if several hundred samples are being analysed and later studied in the form of several thousand separates. A second advantage is the ease with which notes, maps, samples and photographs are all handled in the same series of numbers. The notes and the map stations are complete; i.e., every number in the consecutive series is represented. The samples and photographs carry the numbers pertaining to the stations at which they were taken but there are usually stations at which no samples or photographs were taken and this series is a broken one. Every number which is present, however, fits into one place and *only one place* in the scheme. A third advantage is of importance to persons or institutions collecting large numbers of samples in connection with several projects. The several series of samples, each numbered from 1 up, may be combined in one decimal

series by adding ciphers and key digits at the left. Thus in a five place system the first 5000, a twentieth of the whole, may be divided in any order as occasion arises into number allotments of 2000, 1000, 1000, 400, 300, 200, and 100. Such a system indicates clearly to custodians the position in the collections which should be occupied by the samples collected with a given project. Specimens numbered in the field with the station digits can readily have the project key numbers added at the left when an appropriate block of numbers has been assigned. The following tabulation will illustrate the principle:

00001	to	00999	Project A.
01001	to	01999	" B.
02001	to	03999	" C.
04001	to	04999	Miscellaneous minor projects.
04001	to	04099	Project D.
04101	to	04399	" E.
04401	to	04599	" F.
04601	to	04999	" G.

METHODS AND PRECAUTIONS IN COLLECTING

A sample which has been properly collected is in every respect a miniature representative of the deposit from which it came. From certain types of materials such a sample is obtained with little or no difficulty but in collecting from most of the natural sediments great care is needed to guard against one or more sources of error. If the material is in place in its natural bedded or massive condition the portion which is exposed may be excessively coarse because of the washing away of the finer constituents and retention of the larger pebbles or sand grains in the face of the bank. This is a common condition in vertical or steep gravel banks and leads to a false impression of the abundance of the pebbles as well as to error in the analysis in case a sample is collected without cutting away the surface pebbles. Gentler slopes may be the sites of accumulation of the finer constituents washed from above and samples taken here will show too high a percentage of the finer grades unless care is taken to dig well into the deposit before the sample is collected. In collecting from any situation it is necessary to collect all the material from a given portion of the mass. The accidental falling of material from the bank as the sample is cut away may be highly selective and result in abnormal loss in certain grades unless precautions are taken to catch all the material. In collecting coarse material from a bank a cloth spread to catch the material cut from the cleaned outcrop offers the best procedure. For finer material it is

convenient to hold a scoop-funnel of the type shown in Figure 1 indirectly against the outcrop. The scoop and bag may be held with one hand and the cutting done with a hammer, knife, or other tool with the other hand. In collecting heterogeneous material in which great differences are readily visible to the eye it is desirable to decide, before starting to take a sample, what its limits shall be. This decision is best made by a strictly random method such as taking to a given depth all material covered by a square of cloth laid by chance over the outcrop or by taking all material within a given radius of a random point. Some such predetermined convention relieves the collector of disconcerting uncertainty in regard to re-

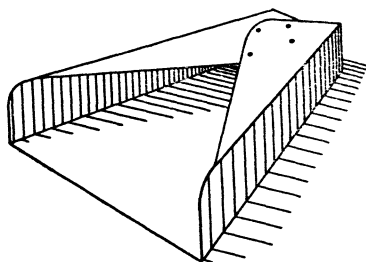


Fig. 1. Collecting scoop funnel
used in filling bags at the outcrop.

taining or rejecting the abnormal material which seems commonly to fall at the last moment or to lie just at the limit of the collecting area. Collecting gravel which is strewn over a beach or samples of pebbles on the surface is exceedingly difficult to perform in an unprejudiced fashion and the most rigorous and unswerving decisions in regard to the area to be covered and the sizes to be considered must be made before starting the collecting. Without these precautions it is inevitable that there will be selective errors based on shape, color, rock material, size or degree of exposure, some of which may be just the sort to vitiate conclusions based on subsequent studies of the sample.

If a sample is taken to represent a given stratum or other small portion of a deposit it is imperative that material from adjacent layers be excluded and the more so the more the materials differ from one another. In case a certain amount of contamination of any sort is unavoidable in practice, note should be made of the amount and probable effect of the foreign material. Samples of sand and gravel collected under water are likely to be washed more

or less free of finer grades of collecting and this condition should be noted to guide later study and interpretation.

PROCEDURE IN SURFICIAL ROCK COLLECTING

The amount of equipment used in this type of collecting depends largely on the means of travel and the distance of the collecting ground from headquarters. Clean samples can be collected with a minimum of equipment if sufficient care is used, but if one is to collect large numbers of samples and is traveling by automobile the work may be done more readily and conveniently and with more uniformity if more extensive equipment is used. The prime requisite is the container. For most surficial collecting, especially if the samples are to be shipped a distance, the cloth bag is most satisfactory. If the pebbles of a gravel are weathered so as to be fragile or if it is desired to preserve the structure of a gravel or other sediment, it will be necessary to wrap the specimen carefully and perhaps to store it in a jar or some other sort of rigid container. For collecting loose sediments a hammer with the transverse chisel type of point is most convenient. If large samples are desired or if samples are to be secured by splitting material cut down from the face of a bank, a sample cloth is needed. This may range from 30" to 6' square according to conditions. If made of oilcloth or other smooth surfaced material it may be cleaned more completely, but for most dry sediments a cloth of drill or denim may be kept sufficiently clean and is more flexible and convenient to handle and is free from surface cracking.

Sheet metal scoops having flat bottoms and low vertical sides at one end and formed to a complete square or round aperture at the other end are very useful both in the field and in the laboratory. (Figure 1.) Several sizes of these having their end apertures corresponding to the sizes of bags used are desirable. The bag may be drawn over the aperture and the scoop and bag thus held with one hand against the outcrop for direct collecting. Pick and shovel are needed where considerable digging is to be done. In collecting material from thin laminae or from the thin surface layers of beaches or rill deposits a small spoon or a putty knife is useful.

Two general types of collecting situations may be distinguished, the vertical or steep bank and the horizontal surface. The former is the more satisfactory from which to collect and in collecting from horizontal surfaces it is best to dig into the deposit sufficiently to

expose its bedding if such exists and collect from the wall of the excavation.

The first operation in collecting from any situation is to clean the face of the outcrop and get back to fresh normal material. In doing this it is wise to clean a considerably larger surface than will be needed for the sample and if the sediment will hold together it is well to clean a channel around the part which is to be collected, leaving it protruding from the rest. In the case of horizontal beds in a vertical bank the strata above and below the layer to be sampled should be cut back if possible, leaving the latter ready to fall without contamination into the scoop, bag or cloth which is placed under it. In the case of a thick layer of uniform material being sampled this procedure may be reversed and the sample made up of several scoops or shovels full of material taken without discrimination from the bottom and sides of a clean hole, taking care that no material falls in from the edges. When a large sample of gravel is taken it is sometimes necessary to pin the sampling cloth tightly at the foot of the undisturbed outcrop, using a couple of spikes or surveyors tally pins.

Samples of heavy concentrates from thin surface layers on beaches and similar situations should be scraped from the surface with a spoon or knife using care not to include material from the underlying layers. In such samples, which are likely to be small in amount, very slight contaminations may introduce considerable errors in the composition.

PROCEDURE IN INDURATED ROCK COLLECTING

The same general principles hold in the collecting of indurated rock as for the loose sediments. If the rock can be disintegrated by treatment with acid or otherwise, it is better to collect a single large sample and analyse the whole of it in the laboratory than to collect a number of small loose pieces which may vary considerably from the normal rock in composition. However, it is commonly difficult if not impossible to disintegrate the rock by artificial means and analysis of a considerable quantity of the weathered debris from the rock is preferable to no examination at all of mechanical composition. If the composition is to be determined in part from study of plane polished surfaces or of thin sections, those cut normal to the stratification are preferable to those cut parallel to it and this consideration should be borne in mind in collecting. In the cases of coarse conglomerates, scale photographs of large exposures normal

to the bedding may be much more valuable in determining mechanical composition than a small specimen which, moreover, offers difficulty in disaggregation.

PREPARATION OF SAMPLES

DISAGGREGATION OF COARSE MATERIALS

No very well defined methods for the disaggregation of strongly indurated coarse sediments appear to have been described.¹² Conglomerates and sandstones which consist of noncalcareous grains cemented by calcium carbonate may be disintegrated by treatment with dilute hydrochloric acid. If a conglomerate is not too strongly cemented it may be broken up and a large fraction of the pebbles saved intact for analysis by sifting. This is best done in stages by hand, using a hammer only as necessary. In some cases disaggregation may be achieved by repeated heating and quenching.¹³ Many gravels, tills and other coarse sediments are only slightly indurated by compacting or incipient cementation and only need thorough wetting, and maceration in water to disaggregate them. In such coarse gravels it is best to handle the process in stages as described in the section on analysis by sifting. The writer has found so much variation in the coarser sediments in the degree and kind of induration that the method of successive fractionation and carrying on the disaggregation by hand, either with the fingers or with a wood or rubber pestle, seems to be as satisfactory as any.¹⁴ In breaking up dry aggregates in sands it is convenient to rub them on a white paper card with the fingers successively removing the fines and changing to fresh cards. The soiling of the card, while it means slight loss, gives a vivid idea of the progress achieved and enables the analyst to follow the process closely. Shaking in a vigorous mechanical shaker disintegrates dry sediments to a considerable extent but can hardly be said to complete the process nor to work successfully on material which would not yield much more readily to wetting and washing.

After a large sample has been mixed with sufficient water to make a soft mud and has been macerated by hand the coarse particles can

¹² Cayeux, L., *Introduction à l'Étude Pétrographique des Roches Sédimentaires*, Paris, pp. 4-5, 1916.

Hatch, F. H., and Rastall, R. H., *Textbook of Petrology, The Sedimentary Rocks*, p. 341, London, 1913.

¹³ Cayeux, L., *Op. cit.*, pp. 4-5, 1916.

¹⁴ Dake, C. L., *Op. cit.*, p. 156.

be taken out by washing the whole on the appropriate sieve. Fine silts and clays of the matrix will reaggregate in drying and analysis is much expedited if a small sample of the fines is reserved before wetting the material so that the fines of the wetted sample may be rejected without drying.

SAMPLE SPLITTING

The splitting of a sample, though it may consist in the establishment of several equal similar parts, usually consists in the separation from the larger sample of one small part which is as nearly as possible identical in composition and other characteristics with the main sample. It may be practiced for a number of purposes among which are the following: (1) Reduction of the size of a large composite or heterogeneous field sample to form the collected sample for the laboratory. (2) Removal from a large sample of one of more normal small fractions for analysis or other study. (3) Successive reduction of fines in the course of analysis. In working with sediments one of the first lessons that is driven home is the strong tendency that exists through the operation of various physical and chemical factors for like materials to become segregated. In splitting samples for mechanical analysis this tendency will be met on all sides and must be largely overcome if success is attained. Not all the details of such segregation are known but a few examples will serve to illustrate the extent to which the tendency is everywhere present. If a small quantity of sand with a few very large grains is shaken in a bottle it is seen that there is a certain amount of separation on the basis of size. When a similar sand is poured from a parallel-sided scoop it is noted that the coarser particles are more abundant adjacent to the sides. If it is poured through a funnel the central portion of the stream differs from the peripheral portions. The sliding and rolling of a heterogeneous sediment down the sides of a pile results in segregation which is apparent to the eye. From these few examples, which may be multiplied almost indefinitely by anyone who will spend a few minutes on a sandpile, it is readily seen that detrital material in which there are diverse sorts of grains cannot be handled without putting in operation some of the factors which bring about segregation. It is equally evident that these tendencies, unless studious attention is given to the problem of thwarting them, will result in abnormal fractions which will vitiate any results obtained from their study.

Most of the splitting or quartering devices which are commonly

used are based on the idea of establishing two nearly equal portions by throwing alternating small portions or streams of flowing material into each. Such devices work satisfactorily if the quantity of material is large in proportion to the size of the larger constituents and if there is a considerable number of these. The type known as the Jones sampler is constructed on this principle and does very satisfactory work. The writer has purchased scoop samplers in which the material is poured on the five-channelled scoop from the solid scoop. The material falling between the channels constitutes one fraction and that falling into the channels another. The solid scoop furnished with some of these outfits is of the same width as five channels and four spaces; thus the abnormal edge portions from the solid scoop both fall into the channels and therefore into one fraction, whereas one should fall on a channel and one on a space. The user of such apparatus must guard against poor designing of this sort since the makers are not always attentive to the correct theoretical principles. Large samplers of the Jones type will do satisfactory work on coarse material with sufficient amounts of material. In splitting small samples of coarse material it seems permissible, and in fact essential, that the coarser grade and perhaps the next be separated out on a sieve and separated by inspection into as many equal and comparable portions as may be required and these portions added to the fractions which have been established by splitting by one of the automatic methods. For any grade of large fragments in which there are so few pieces that they may readily be inspected at a glance this method of splitting is better than one which depends on the laws of probability since these operate to the end here desired only when numbers are large.

The method of splitting known as quartering, as applied to the collecting of coal and ore samples, consists of the formation on a sample cloth of a conical pile of well mixed material which is cut into quarters by two right angled separations and the alternate quarters rejected. The remaining two quarters are again mixed by lifting and rolling the material on the cloth, alternately forward and backward from left and right. A new conical pile is again quartered as before. The procedure is continued until the sample is reduced to the size required. After trying this method with gravels the writer is of the opinion that it is much less successful in maintaining normal fractions for other kinds of analysis. The technique of coal sampling specifically requires crushing of the large

sample to a half inch mesh which not only insures that there be a large number of fragments but also that large fragments be eliminated. The main purpose of gravel collection for mechanical analysis forbids the use of these two principles which are essential to the quartering method. The latter method works well with relatively homogeneous materials, but these are also well handled by most of the other methods.

A coarse sediment which has been well mixed by stirring and beating in a pan or on a cloth may be split with fair accuracy by throwing successive spoons or scoops full into alternate fractions as it is transferred from the pan or cloth. In this method care should be taken to avoid the systematic dipping of the spoonful for the two fractions from different parts of the original mixture. The spoon or scoop should be filled quite as monotonously as possible from the mixture and emptied alternately to one side and the other.

Well mixed material which is poured in a broad stream from a pan is reasonably well split if the stream is made to flow half into one container and half into another adjacent to it. The stream should be made to flow symmetrically with the edges as nearly as possible.

It will be noted that nearly all the methods mentioned involve splitting the sample into halves and then one of the halves into quarters and so on. This is an essential part of the process. Any attempt to separate the sample into a large and a small fraction at once is likely by the nature of necessary devices to bring about some segregation favoring the accumulation of coarser material in one fraction or the other and vitiate the results.

ANALYSIS BY SIFTING

GENERAL PRINCIPLES

In practice, analysis by sifting can be applied to the separation of sediments down to a fineness of about .05 mm. or .002 inch. From this size up to 10 cm. or about 4 inches, sifting can be conveniently accomplished in a series of testing sieves. Cobbles larger than this size are not ordinarily present in numbers in the samples analysed by the geologist and can be discriminated by individual measurement.

Some investigators in the past have advocated the use of sieves with round holes. These have the advantage that the sizes of the openings can be determined with great uniformity and that they

may be readily made from sheet metal without elaborate special equipment. It has also been urged in their favor that a round hole is naturally more appropriate for the separation of the somewhat rounded particles than is any other shape of opening. In spite of these considerations the woven wire sieve with square openings has so many points in its favor that it has been generally adopted. Woven wire cloth is now made in a very great variety of sizes of opening, and diameter, and material of wire. Double crimped wire cloth keeps its original uniformity of spacing so successfully even with considerable rough handling that one of the former objections to the woven wire sieve has been overcome. The woven wire cloth can be made with much smaller openings than is practicable in the sieve made by punching or drilling round holes in sheet metal.

Some workers advocate the use of bolting cloth in clamp rings because of the ease with which new and clean cloth may be inserted. This method is doubtless of value when samples of sands of diverse sorts are to be studied for mineral content and it is desired to use extreme care to avoid contamination, but it seems hardly applicable to mechanical analysis to a grade scale of the sort suggested below.

As to the shape, it is probable that the round hole should be regarded as slightly more appropriate. However, since the minor cross-sections of most of the particles passed by any sieve are neither round nor square but more or less intermediate, it is probable that the difference in amount between the material passed by square and round opening sieves of the same diameter of opening, is very small. To be sure, the writer does not consider that analyses made in the two types of sieves would be interchangeable but merely that in the proportions of materials in successive grades one type of analysis is probably as good an approximation to the ideal hydraulic classification as is the other.

CHOICE OF GRADE SCALE

The ideal representation of mechanical composition is a smooth curve showing the continuous distribution of sizes in their proper proportions from one end to the other of the range. Such a result is only to be attained by careful individual measurements on all the constituent fragments of the material in hand. Except for purposes of illustration or investigation as applied to a very limited amount of material, such procedure is not practicable and less laborious approximate methods must be chosen. The most obvious scheme is to divide the material into classes, determining the amounts in the

several classes and thus indicating the distribution of the material in point of sizes of particles. If a large number of classes is established the results will approach those attained by individual measurements, but at the same time the operation becomes more time consuming. Whether a large number of classes of small range between their upper and lower size limits or a small number of large range are to be used must be determined according to the use to which the analysis is to be put and whether the greater expense of the former alternative is justified by the greater accuracy.

In choosing the classes into which the material is to be divided the limits of the several classes may be set according to a number of different considerations. In the case of materials for commercial use certain definite size limits governed by precedent or the capacity of equipment may be the critical limits in the analysis. Too often, in the case of geologists making mechanical analyses, expediency has governed and the grade scale has been determined by the series of sieves which chanced to be available with little attention to the fitness of the several size limits. The result has been that analyses have been made to a great variety of grade scales, many of which were ill adapted to the purpose in hand and all of which, because of the great variety, have hindered direct comparison. No argument is needed to indicate the great desirability of the use of the same grade scale by investigators who are working in the same general field, such as geology. In choosing the scale for general use it is well to consider those which have been used in the past. These are of several sorts as follows:

In the following table are given four types of grade scales which have been used in making mechanical analyses.

TABLE OF GRADE SCALES¹⁵

A	B	C	D
1.000"	1.000 mm.	2.33 mm.	8. mm.
.500"	.500 "	1.66 "	4 "
.250"	.250 "	1.17 "	2 "
.100"	.100 "	.833 "	1 "
.050"	.050 "	.589 "	1/2 "
.025"	.025 "	.417 "	1/4 "
etc.	etc.	.295 "	1/8 "
		.208 "	1/16 "
		.147 "	1/32 "
		.104 "	etc.
		.074 "	
		etc.	

¹⁵ Dake, C. L., *Op. cit.*, p. 152. Holmes, A., *Op. cit.*, p. 197.

These scales are tabulated in this form not to show comparisons between them but to show the ratio and starting point characteristic of each. Scales A, B, and D have simple integer starting points, one inch, one millimeter and one millimeter respectively. Scales A and B are hybrid scales in which two different ratios are used to secure an approximately uniform ratio and at the same time to make every third grade limit coincide with a decimal submultiple. Scales C and D are equal ratio scales (within limits of error in construction of sieves), the ratios being the square root of 2, and 2, respectively. Scale C starts from the exhaustively calibrated 200 mesh sieve used as the basis of fineness specifications of Portland Cement. Scale D combines the 1 millimeter starting point with a uniform ratio of 2.¹⁶

There have been numerous variations of these types used in practice and there are a number of nonuniform but approximate geometric scales represented by the systems of sieves in which the coarseness is designated by the number of meshes to the inch. Since in the past and to some extent at present the size of wire used in making these sieves has not been uniform there is much variation in the actual opening sizes and a number of different grade scales result.¹⁷

In too many instances in the past and occasionally even at the present time the sizes are indicated only by stating the mesh, a designation which is next to useless unless the critical data are given elsewhere in the paper and in that event needlessly cumbersome.

In all the scales which have been used in the past there is tacit recognition of the essential correctness of the constant ratio of geometrical scale. The arguments in favor of such a scale have been stated by the writer and others elsewhere and need not here be repeated.¹⁸ Several possibilities present themselves in the choice of ratio, of starting point and of system of mensuration. Scientific work is now practically all carried on in metric units and this system seems best adapted to the mechanical analysis grade scale. One of the cardinal points of the metric system is its expansion on the

¹⁶ Cayeux, L., *Op. cit.*, pp. 34-36, Paris, 1916.

Mohr, E. C. Jul., Bulletin In Département de L'agriculture aux Indes Néerlandaises, No. 16, Buitenzorg, 1910.

¹⁷ Milner, H. B., Introduction to Sedimentary Petrography, p. 18, London, 1922.

¹⁸ Wentworth, C. K., A Scale of Grade and Class Terms for Clastic Sediments: Journal of Geology, Vol. XXX, p. 382, 1922.

decimal basis. Desire to use certain of the simple decimal fractions has led to such scales as B in the table above. Scales such as the following in which the ratios are small integer roots of 10 have been suggested by various investigators but so far as known to the writer have not been used in practice.

Ratio $\sqrt{10}$			Ratio $\sqrt[3]{10}$		
E.	10.000	mm.	F.	10.000	mm.
	3.162	"		4.641	"
	1.000	"		2.154	"
	.3162	"		1.000	"
	.1000	"		.4641	"
	.03162	"		.2154	"
	.01000	"		.1000	"

These scales have the advantages of return to the submultiples of ten at uniform intervals and that the number of decimal sequences to be carried in mind is small. On the other hand, it is impossible to express them in common or vulgar fractions.

The scale made up of multiples and submultiples of 2 starting from 1 millimeter is probably most readily visualized of all. (Scale D.) The ideal scale would be possible if our system of numeration were a sexadecimal system instead of the arabic decimal system. Then we should be able to use halves, quarters and eighths of the

TABLE I
THE GRADE TERMS

The Pieces	The Aggregate	The Indurated Rock
Boulder	Boulder gravel	Boulder conglomerate
256 mm.		
Cobble	Cobble gravel	Cobble conglomerate
64 mm.		
Pebble	Pebble gravel	Pebble conglomerate
4 mm.		
Granule	Granule gravel	Granule conglomerate
2 mm.		
Very coarse sand grain	Very coarse sand	Very coarse sandstone
1 mm.		
Coarse sand grain	Coarse sand	Coarse sandstone
1/2 mm.		
Medium sand grain	Medium sand	Medium sandstone
1/4 mm.		
Fine sand grain	Fine sand	Fine sandstone
1/8 mm.		
Very fine sand grain	Very fine sand	Very fine sandstone
1/16 mm.		
Silt particle	Silt	Siltstone
1/256 mm.		
Clay particle	Clay	Claystone

fundamental sexadecimal ratio and combine simplicity in visualization with simplicity of computing and notation.

The best compromise at present possible seems to be the use of the geometrical ratio-scale which may more simply be designated as the 1-2-4-8 mm. scale. The engineer scale which is based on the highly standardized but arbitrary size of opening in the 200 mesh sieve seems to the writer to be of too arbitrary a character and to entail needless complication in the decimal fractions by which the several limits must be designated. The names and limits of the several grades established by the 1-2-4-8 mm. scale are indicated in the table below previously published by the writer.

EQUIPMENT

The following outline indicates the range of equipment which is convenient in analysing sediments of sifting.

Sieves and accessories	{ Fitted sieves Covers Pans Blank sieve rings Wire squares Mechanical shaker Timing clock
Weighing apparatus	{ Balance, beam Balance, portable assay Balance, spring Graduated cylinder
Handling apparatus	{ Bag funnel scoops Tube funnel trays Metal pans Spoons Funnels
Splitting apparatus	{ Sample splitter Scoop Pans, square

Storage accessories	{ Cloth bags Screw top glass jars Metal pill boxes Glass specimen vials Corks Gummed labels Tube blocks
Washing apparatus	{ Jars and cylinders Rubber tubing Glass tubing Rising current washers
Miscellaneous accessories	{ Brushes Squares of paper Rubber stamps for notebook tabulating

Testing sieves consisting of woven wire cloth soldered into substantial stamped brass rings may be had from a number of makers. Some of these makers¹⁹ are in a position to furnish sieves with openings conforming very closely to the scale here recommended when so ordered. These sieves are made so as to fit tightly one above another and are available in several diameters and heights. The writer has found that two sets, an eight inch series running from 64 to 2 millimeters, and a six inch series running from 1 to 1/16 millimeter are convenient since it is rarely desirable to run the analysis of a sediment ranging from 32 to 64 millimeters down to 1/8 mm. or less in one stage. Another set of six inch sieves running from 8 mm. to 1/16 mm. is convenient for those samples which lie in this range and may best be run in one stage. The six inch sieves are quite large enough for materials under 1 millimeter. In traveling, the individual six inch sieves can be packed in the spaces of the 8 inch series with much saving of space.

A pan and cover are essential with each set of sieves and an extra pan or two are very convenient when handling the individual separates while leaving the main sieve pile standing by. Blank sieve rings, which can be obtained by special order from the makers, are useful in increasing the capacity of any given sieve in handling large samples of the coarser gravels. In ordering these one should

¹⁹ Newark Wire Cloth Co., Newark, New Jersey; Multi Metal Co., 799 East 139th St., New York City; W. S. Tyler Co., Cleveland, Ohio.

specify that they be crimped together and in every way completely assembled except with the wire cloth left out. When analysing sediments containing a few fragments larger than the largest grade isolated by the sieves, several large wire squares conforming to units of the grade scale are useful in testing these large pieces.

If large numbers of analyses are to be made a mechanical shaker is almost indispensable. The accuracy of separation is very greatly increased, results are standardized to a degree impossible in hand shaking, and very heavy samples may be handled in one stage which in hand shaking would have to be worked through grade by grade. With an automatic timing clock such an instrument accomplishes in a day's time shaking which would take at least a week by hand methods and at the same time leaves the operator free to perform the weighing and other operations of analysis. Mechanical shakers may be purchased from the makers or may be constructed in any well equipped machine shop. A shaker should be so designed as to combine lateral and rotary motions with rather vigorous jarring.

The balances used in mechanical analysis should be of the substantial laboratory sorts rather than precise analytical balances, since convenience, speed of operation and general staunchness are of more importance than great accuracy. Those of the three beam design with sliding weights by which the tens, units and fractions of grams are determined are satisfactory. Small compact portable assay balances are convenient for field use with small samples and spring balances have been used by the author in field analysis of coarse sediments. In working with rather homogeneous materials, such as sands of low size range in the field, it is probable that proportions could be determined with adequate accuracy by volumetric means, though the writer does not know that this method has been used in practice.

If much analysis is to be carried on several types of scoops and funnels will be found useful and may be readily made by any sheet metal worker. The funnel scoop shown in Fig. 1 is convenient in filling bags from the outcrop or from sieves or pans. Low-sided square or triangular trays slightly larger than the sieves and having one open corner are convenient in transferring sand grades from the sieves to the glass vials in which they are stored. An assortment of spoons and funnels adds to the convenience of handling.

If large numbers of samples are to be analysed they are handled most expeditiously by separating operations and several must be at

various stages of completion in the laboratory at the same time. In this case many containers will be needed for temporary use. Small metal pill boxes are useful in this connection and for the larger and coarser separates round flat-bottomed pudding pans or basins with flare sides are recommended. These are easily cleaned, will withstand the moderate heat used in drying sediments, and by nesting many of them may be stored in small space when not in use.

One or more sample splitters will be needed and if there is a great range in the coarseness of the samples handled these should be of both large and small sizes. The Jones sampler is to be recommended or for combined field and laboratory use a folding splitter based on the same principle will be more convenient. A number of square pans should be provided for use with the splitter.

In the study and subsequent storage of sediments which have been mechanically analysed large numbers of containers are needed. Since many of the materials are fine grained they must be stored in tighter containers than are needed for many other types of rock specimens and like other specimens for scientific study and reference, must be carefully labelled. If permanent storage shelves or cases are available screw top glass jars are the most satisfactory containers for the larger samples. These are rather expensive in large numbers and it may be necessary to use cloth bags for these samples, and in any event the latter are preferable for field collecting. Glass shell vials are convenient and inexpensive for storing samples of materials not coarser than 8 mm. up to 25 or 50 grams in amount. These may be had in various sizes and are closed with short corks and stored vertically in holes in wood blocks. The writer has found that it is more satisfactory to design the blocks and case drawers so that a certain number of the blocks fit in each drawer than to design a single large perforated tube holder for each drawer. With the former scheme a small number of vials together with the block may be removed for inspection. In the laboratory at the University of Iowa each block accommodates 50 one-half inch vials in 5 rows of ten each. Each drawer of a case accommodates eight blocks in 2 tiers of 4 each, thus storing a total of 400 tubes one-half inch in diameter and two inches long.

In washing sediments an assortment of jars and cylinders and glass and rubber tubing are convenient. In a laboratory in which much mechanical analysis is done a rising current washing machine as a permanent installation will save the labor incident to rinsing the various sediments by hand methods.

Several brushes with soft bristles are useful in transferring fine sediments from one container to another and may sometimes be used in cleaning fine sieves. Squares of paper of several sizes will be found of occasional use even in a laboratory well equipped with containers of various sorts. In recording the results of analysis a rubber stamp bearing in a vertical column the designations of the several sieve grades is convenient in blocking out the entry in the notebook.

PROCEDURE

In describing the procedure of sifting it will be most convenient to follow an order which is mainly chronological, starting with types of analysis of coarse sediments which are sometimes carried out in the field and proceeding thence to the laboratory technique.

When a sample of coarse material ranging to 64 mm. or more and amounting to 30 or 40 kilograms has been collected on a sampling cloth and is not needed for exhaustive laboratory study, a part of the analysis may well be accomplished on the spot. The sample is first weighed as a whole, using a spring balance attached to the four corners of the cloth. The known weight of the cloth should be recorded along with the gross weight. Then, working on the cloth, all pebbles and cobbles over a convenient sieve size should be separated from the finer material. In many instances this separation can be accomplished without attempting to pass all the material through the sieve in question but merely working through the material and testing doubtful pieces on the sieve. The coarser fraction should now be cleaned, if need be washed and dried, run through the coarse members of the sieve series and then separated weighed by spring balance or placed in bags for laboratory weighing. The material washed or cleaned from these fragments may be discarded if most convenient rather than added to the fine fraction. If desired, measurements of shape and notes of lithology and color of the larger separated cobbles may be made and after weighing they may be discarded.

The fine fraction remaining on the cloth which usually amounts to a large percentage of the whole sample and which is relatively much more homogeneous than the original sample, may now be quartered or otherwise split down to a sample of size appropriate to the coarseness of the larger remaining fragments. If, for example, the 4 mm. sieve was used in making the primary separation the fine fraction may be split down to about 1 kilogram and the remainder rejected.

The part retained will be weighed and analysed in the laboratory. The total weight of the fines below 4 mm. is determined as the difference between the total sample and the total of the cleaned grades above 4 mm. It will be noted that the only operations which must be carried out at the outcrop are the weighing of the total sample, the separation of the sample at 4 mm. or any other convenient limit, and the splitting of the fine fraction down to portable size. In many instances the coarse grades will not be of great weight and the sample will be reduced in weight by as much as 75 or 80 per cent by throwing out the bulk of the fine fraction in the manner described. Furthermore, in order to do this no more equipment is needed than a single sieve or in a pinch a single accurate wire square.

In analysing a large sample of coarse sediment in the laboratory, the process should be carried on in stages in a similar fashion to the field procedure. If the material is fairly dry and not extensively aggregated, the 2 mm. sieve may be made the separating limit; otherwise a coarser one must be chosen. The entire sample is poured on the pile of sieves at one time if it is not too bulky. There may be insufficient room in the pan under the 2 mm. sieve for the fine fraction, in which case this will need to be successively removed. Coarse separates which are too large in bulk for one sieve space may still be retained by adding a blank sieve ring to the pile at the proper place. After all the material has been added and the pile has been shaken to secure a rough separation into grades and determine the approximate amounts, it is ready for the final shaking by hand or in the mechanical shaker. If the sample is dry and clean enough so that practically no fines will remain with the coarse grades as aggregates or incrustations, the whole sample need not be weighed before starting the analysis but in most cases this should be done.

If a mechanical shaker is available the shaking may be very quickly accomplished. If hand shaking is necessary the separate coarse grades are best shaken one at a time, using a cover and pan with the single sieve and starting with the coarsest grade. It is not practicable to establish any standard time of hand shaking for materials of this sort. With a sieve containing 5 or 10 eight to sixteen millimeter pebbles the completion of the sifting is apparent by inspection. As one proceeds to finer grades the end of the process is less sharp. Since the condition of sediments varies so greatly the best practice seems to be to continue shaking until the amount com-

ing through the sieve is negligible for the purpose in view.²⁰ This is best determined by emptying or changing the pan after the major part of the fines has come through and shaking successively over an empty pan for a number of equal short periods. For fine sediments the completion of the sifting process is a practical impossibility, either by hand or by machine, and the end point must be determined according to the accuracy desired. The writer has used a period of 5 minutes for machine shaking on a series of coarse sediments and achieved a satisfactory separation for his purpose. The subject of accuracy will be considered more at length in the section on sources of error below.

After shaking, the coarse grades should be cleaned and weighed. The fine fraction must be weighed if the total sample weight was not determined or if the process is to be checked. This portion is then split to a size suitable to the size of its coarser grades. The analysis of a part of the fine fraction is accomplished in a manner similar to that described above. The principal difference is that in shaking by hand a larger part of the whole shaking may be done while handling the entire pile of sieves. Any sediment in which a considerable number of lumps or aggregates withstand the shaking process and remain with coarser grades should be washed or otherwise disaggregated. By weighing the whole sample and determining total fines by difference the more troublesome part of the washing process, the recovery of the fines, may be eliminated provided a small fraction is retained before starting the washing process.

No method of cleaning sieves is known which is rapid and effective. Some of the grains may be removed from the sieves by rubbing from the bottom side with a cork. Jarring or striking the ring with the hand in a direction diagonal to the wires will dislodge some but not all of the grains. A stiff brush may sometimes be used to advantage. Complete cleaning is achieved only by using a fine-pointed implement on the individual grains and taking care not to injure or displace the wires.

In making critical mineralogical studies the best procedure appears to be the use of bolting cloth or of small wire sieves such as 2 inches in diameter which one may keep absolutely clean by going over each sieve with a pointed tool.

The cleaned separates should be weighed on removal from the

²⁰ Goldman, M. I., *Petrography and Genesis of the Sediments of the Upper Cretaceous of Maryland*, p. 121, Baltimore, 1916.

sieves and then rejected or stored as the case may be. In general, weights should be determined to the order of the nearest 1/1000 of the whole sample analysed in the given stage. For very careful work in checking technique or with very homogeneous material somewhat more accurate weighing is desirable.

The amount of material needed for most satisfactory analysis varies somewhat with the composition of the material as well as with the coarseness. The amounts indicated in the last column of the table on page 10 are minimum amounts for material down to about 8 mm. Below that limit the amounts most convenient for analysis are shown in column 2 of the table. It may be suggested in general that the material lodging in any one sieve should be small enough in amount so that at least half the sieve surface is free at the end of each shaking oscillation. Sifting is a very slow and probably much less accurate process when the material on a sieve covers it deeply throughout the shaking.

The annotated computation outlines given below in the section on computing and plotting will serve as tabular summaries of the analysis procedure under several different conditions.

SOURCES OF ERROR

A mechanical analysis is a means of determining the mechanical composition of all or part of a sedimentary deposit. If the composition shown by the analysis is not identical with that of the deposit the analysis is in error by the difference. The composition shown by analysis may be accurate as representing the sample from which it was made and still very inaccurate as representing the deposit from which the sample came. A tabular synopsis of the various sources of error in mechanical analysis is given below.

Errors resulting from the geologist's inability to locate the sample properly are probably large. Especially if the sample is taken for the purpose of representing the typical composition of a deposit, it is likely to fall short of its purpose. The writer believes that there is a strong tendency in attempting to collect a *typical* specimen to collect what is more properly an *ideal* specimen. Other errors of the collecting process can be largely reduced by care in the technique. It is believed that with the present excellence of woven wire cloth errors due to variations in sieve openings from uniformity or from the ratings of the makers are relatively small and negligible compared to the errors arising from the inability of the geologist to collect, even from the same outcrop at different times,

two identical samples. Elaborate tests of the performance of a series of sieves made by a reliable maker do not seem to the writer to be crucial in assuring the reliability of analyses made thereby when so much larger errors almost without exception are present as

ERRORS IN MECHANICAL ANALYSIS

	Source	Result
C O L L E C T I O N	Sample not well located.	General error.
	Sample too small.	Large errors in coarse grades.
	Outcrop not well cleaned.	Increase in either fine or coarse grades.
	Selective accidental loss in collecting.	Decrease in either fine or coarse grades.
	Subsequent loss from container.	Decrease in either fine or coarse grades.
P R E P A R A T I O N	Unsound splitting method.	Increase in either fine or coarse grades.
	Faulty splitting practice.	Increase in either fine or coarse grades.
	Splitting to too small fraction.	Large errors in coarse grades.
	Loss of fine grades on cloth or from blowing.	Decrease in fine grades.
	Error in assumption that fine grades washed from aggregates are normal.	Probable decrease in finest grades with increase in intermediate.
A N A L Y S I S	Errors in sieve opening ratings.	Local errors between grades.
	Nonuniform sieve openings.	Local errors between grades.
	Incomplete shaking.	General increase in coarseness indicated
	Loss of fine grades by lodgment in sieves or elsewhere.	Decrease in finest grades.
Computation and Plotting	Errors in weighing.	Local large error, small general error.
	Errors due to use of slide rule.	Small local errors.
	Errors in plotting.	Small local errors.

a result of unknown infelicity in the choice of the sample. In the case of the standardization of the 200 mesh sieve for engineering specifications the situation is quite different for here a highly uniform artificial material is being handled of which the mechanical composition as delivered is critical.

There is another viewpoint in considering the accuracy of mechanical analyses. The means of interpreting mechanical analyses do not seem likely in the near future to reach an excellence capable

of taking account of very small differences in mechanical composition. For purposes of interpretation the writer believes that errors in any grade amounting to less than $1/4$ per cent of the whole sample times the square root of the percent of the grade (an arbitrary rule) may be regarded as negligible. Figure 2 shows the plotted pyramids for two analyses differing within this range. In a two-grade analysis if differences less than the amount stated are con-

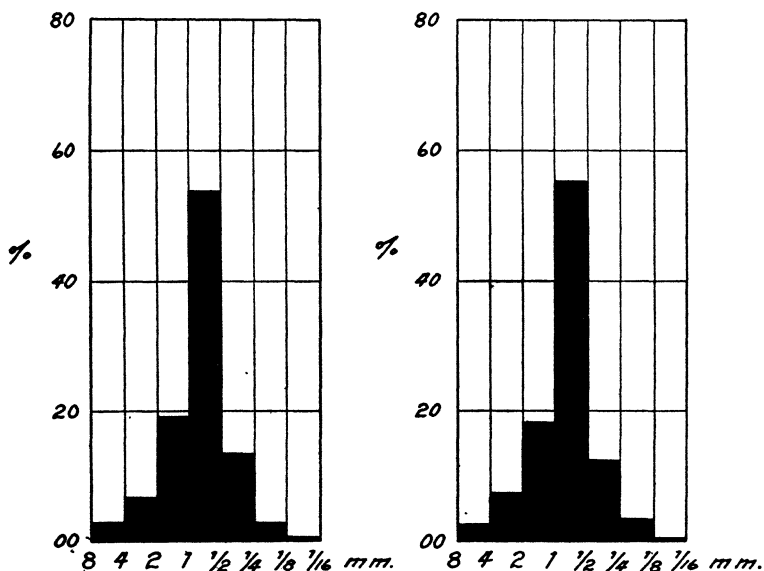


Fig. 2. Composition pyramids or histograms of two analyses differing by the limits described above.

sidered negligible there are still approximately 100 types of composition possible, disregarding those where one grade is less than 1 per cent. Similarly in a three-grade analysis there are approximately 5,000 types and in a four-grade analysis are well over 150,000 possible types of mechanical composition of which a large fraction would be likely to occur in natural sediments.

The writer does not wish to advise against improvement of the accuracy of the sifting operation of mechanical analysis but he believes that the results at present attainable with reasonable care in the technique are so much in advance of the reliability of the collected samples and in advance of present methods of interpreting the analyses after they have been made that the principal emphasis in making for improvement should be placed at the two last named

points. It seems, for example, that it would be much more profitable to collect and analyse in a fairly accurate and expeditious fashion 100 samples, computing the results by slide rule and presenting them in graphic form than to spend the same time on 25 samples, running analyses in duplicate, weighing to one more place of decimals and presenting the results to hundredths rather than tenths of a per cent.

ANALYSIS BY COUNTING

GENERAL STATEMENT

Under this heading are considered a number of methods which have in common the feature that the size of each fragment is determined by some sort of direct measurement. None of these methods may be considered preferable to the method of screening when the proper equipment for the latter is available and it can be applied, but are rather to be regarded as supplementary under exceptional conditions as applying to sediments beyond the range of screening.

ESTIMATING COMPOSITION IN THE OUTCROP

It is sometimes desirable to make an estimate of the relative abundance of boulders of different sizes in a coarse gravel or till and such is essentially an estimate of mechanical composition. It is sometimes possible to accomplish this by measuring the boulders in the reject pile of a commercial gravel pit where the large boulders encountered in working a known volume of gravel have been piled at one side to get them out of the way. More commonly such an estimate must be made from the outcrop and in such a case a large, fairly plane exposure normal to the bedding is most suitable. The procedure used by the writer is to select in the given outcrop a series of cobbles and boulders as reference sizes, one for each grade. These may be chosen to represent the mean size of the grade such as the series 90, 180, 360, 720, 1440 millimeters,²¹ or the limiting sizes of 64, 128, 256, 512, 1024 millimeters. They should be chosen by actual measurement to conform as closely as possible to the square mesh sieve series. After marking these with chalk or otherwise the estimate should be made by standing well back from the outcrop and counting all those cobbles and boulders which appear to belong to each grade. In making use of such a count several principles should be borne in mind. First, the apparent size as protrud-

²¹ Consisting of the series 64, 128, 256, etc. multiplied by $\sqrt{2}$ respectively.

ing from the outcrop is not the real size, being often smaller and in fewer instances (case of a broadside view of an elongate boulder), being larger. Second, the larger boulders which appear in the outcrop represent a much larger volume of the material than do the smaller cobbles which appear in the same outcrop. The first principle named probably does not introduce errors which would be regarded as large in an estimate of this kind since the general convexity of the exposed portion of the boulder will enable the observer on the average to place a given boulder in the correct grade even though the area exposed is much less than the true cross-section. The second principle must be considered more in detail. An adequate theoretical study of the relative probability of retention in the outcrop of large and of small boulders would be extremely complicated and the factors involved would have different values for a host of different rocks. For the present purpose it will suffice to eliminate a number of these by assuming a similar behavior for large and for small boulders. For example, any boulder may be said to be represented in the outcrop if, protruding sufficiently from the outcrop to be recognized as belonging to its proper grade, it is still well enough supported and held to remain in place. Similar retention in large and small boulders may be defined as the condition when the range of retention from a given percentage of linear protrusion needed for recognition to the larger percentage of linear protrusion when the boulder falls is a constant fraction of the average diameter of the boulder regardless of its absolute size. If this be the case then the boulders of several grades which are present in the outcrop represent volumes of material which stand in the ratio of the linear dimensions of the several grades. This approximate assumption will be made clear by reference to the following computation schedule.

In using this method of estimate the results obtained by methods so far described are relative and some absolute measure must be had to permit expression as a partial mechanical analysis. Perhaps the best method of securing this is by estimating the linear thickness of the zone of retention for one of the coarser grades by inspection. A grade in which there are a number of boulders should be used rather than to use very few boulders of extreme size. This measure times the length and height of the exposure will give the volume of which the number of boulders of the grade in question are a proper part

and the volumes for the other grades are scaled from this, using the proportion principle stated above.

This method is, of course, not a quantitative one in the strict sense, yet it is believed that the present proper trend in geology is toward quantitative points of view and methods of expression and that estimates of this sort are of much value when undertaken by

TABLE SHOWING REDUCTION OF FIELD DATA IN ANALYSIS BY COUNTING AT THE OUTCROP²²

Grade sizes	Number of pieces	Number in unit volume	Total volume of grade ²³	Per cent of total
512-256 mm.	3	3	12188	7.4
256-128 mm.	18	36	18432	11.1
128- 64 mm.	29	112	7168	4.4
64- 32 mm.	15	120	960	.6
32- 16 mm.	21	336	336	.2
			39084	23.7

a competent observer who has the necessary theoretical principles in mind when making the observations and making the subsequent computation.

MEASUREMENTS OF THREE DIAMETERS

Measurements of three diameters are sometimes made in the course of studies of roundness or other shape characteristics and may be of subsequent value in separating the pebbles or cobbles into grades. In doing this the average diameter may be used for compact nearly equidimensional fragments, but use of the small cross-section (lesser times intermediate diameter) is more accurate for elongate forms.

²² Values in column 3 are obtained from those in column 2 by multiplying by the multiples of 2 starting from the top, i.e., 1, 2, 4, etc. Column 4 is derived from column 3 by multiplying by cubes of the powers of 2; i.e., 1, 8, 64, 512, etc.

²³ Units are volumes of mean pieces of 32-16 mm. grade or

$$\frac{16 (1.414)^3}{6} \times 3.1416 = 6,066 \text{ cu. mm.}$$

Unit volume is in this case an area of three square meters to a depth assumed as approximately the mean diameter of pieces of the larger grade; i.e., 35 cm. or practically 1/3 meter. The volume of the grades estimated is the product of 6,066 cu. mm. by the total of column four and is .237 cubic meters or 23.7 per cent of the whole. The composition of the remaining 76.3 per cent must be determined by sieve analysis of a sample of the minus 16 mm. matrix.

ANALYSIS BY WEIGHT

The cobbles and pebbles of a coarse sample may be sorted into grades on the basis of weight fairly rapidly by using a spring balance and pan. After determining the grade limits by weight a paper scale having only three grade limits marked in strong lines may be attached to the face of the balance. Speed is increased by making a preliminary rough sorting by inspection, thus permitting the weighing of like sizes in close succession. If the range is great two or more balances of different capacities will be needed.

MICROSCOPIC COUNTING

The writer has had but limited experience in this type of mechanical analysis. Certain points in this limited experience seem worthy of mention. Counting is best done on a ruled surface or using a ruled eyepiece. For material over about $1/8$ mm. paper ruled in millimeters has been used to good advantage as a background. Fine ruled gratings on glass for use on the microscope stage may be had of dealers in accessories. Eyepiece gratings have the disadvantage that they do not commonly conform to the grades used and if one is provided for use with one objective it will be of odd size if used with another. To get around various of these difficulties the following method is suggested. All microscope fields which are to be analysed are projected onto a frosted or ground glass surface above the microscope in the manner used for photomicrography. On this surface are drawn permanently the lines of a grating of appropriate size. By changing the distance of projection and the objectives it is practicable to enlarge grains of sediment of all grades to a standard image size and make all counts on the ground glass at this size, which can be large enough to greatly reduce eye fatigue. By the use of ordinary camera lenses as well as microscope objectives, all grades, even those which are readily estimated by direct inspection, may be projected to a standard image size, the larger fragments being reduced. Thus a whole sample may be subjected to the same technique and the inevitable break which would attend errors of judgment if the work were partly megascopic and partly microscopical is eliminated. Another advantage of this method is that the grains counted may be checked off on the ground glass with a pencil thus lightening the fatigue of sustained attention in ordinary microscopic counting.

ANALYSIS BY ELUTRIATION

FOREWORD

In the first outline of this paper it was intended that the analysis of fine sediments by elutriation should be treated at length. Progress of the work showed the inadvisability of attempting a detailed treatment at this time and the following brief outline is here presented as a supplement to the methods applicable to coarse sediments.

OUTLINE OF METHODS

By some students the term elutriation is confined to separation of grains in a rising current apparatus, but by others it is also applied to separation by settling in a static column. The writer prefers the latter usage. Apparatus for elutriation has been described by a number of investigators and these descriptions need not be presented here. Four principal types may be recognized as follows:

1. Jars and cylinders for simple decantation.²⁴
2. Simple tubes for rising current separation.²⁵
3. Multiple tube series for rising current separation.²⁶
4. Recording subsidence machines of the Oden type.²⁷

Each type has points of merit. The simple decantation jars and cylinders are simple and easy to operate and with repeated washing results are as accurate as those derived by any other technique. Need for repeated washing is eliminated in the continuous current devices (2 and 3). In the Oden machine the true composition curve is deduced by mathematical analysis of the curve of settling. The continuous current devices have the disadvantage that the axial velocity and marginal velocity in the tube differ greatly and the exact conditions of separation at different temperatures are not known. The principal disadvantages of the Oden machine, as they appear to the writer, are the expense of construction and installation and the labor of computing results.

²⁴ Goldman, M. I., *Petrography and Genesis of the Sediments of the Upper Cretaceous of Maryland*, pp. 169-170, Baltimore, 1916.

²⁵ Holmes, A., *Petrographic Methods and Calculations*, p. 215, London, 1921.

²⁶ Holmes, A., *Op. cit.*, p. 209.

Hatch, F. H., & Rastall, R. H., *Textbook of Petrology, The Sedimentary Rocks*, pp. 342-357, London, 1913.

Cayeux, L., *Op. cit.*, pp. 36-45, 1916.

²⁷ Oden, Sven, *Studien über Tone*, 2, *Automatisch registrierbare Methode zur mechanischen Bodenanalyse*, Bull. Geol. Inst. Univ. of Upsala, pp. 15-64, Upsala, 1919.

GRADE SCALES

All methods of elutriation involve the problem of hydraulic values of particles of varying size, shape and density at various temperatures. This problem has been approached by many investigators but no adequate determinations have been made of the effects of shapes of particles in modifying their velocity of fall through water.²⁸ Data given by different students show large variation.²⁹ Theoretical values, according to Stokes law, differ from any of the empirical values. Theoretical hydraulic values for spheres follow two different laws for large and for small particles. Large particles fall in water with velocities proportional to the square root of the diameter. Small particles fall with velocities proportional to the square of the diameter. (Stokes law.) Both rates depend on certain constants derived from the densities of water and the particle and the viscosity of water at the temperature in question. In the case of large particles viscosity is negligible; in that of small particles inertia becomes negligible. In the zone between 1.55 mm. and 0.2 mm.³⁰ for particles of the density of quartz both factors are important and the velocities undergo a transition from those of the square root law to those of the square law.³¹

In the case of a study of silts and clays in which the entire sample can be separated by elutriation, the grades may best be designated by the limiting falling velocities in millimeters per second, using a uniform ratio series like the powers of 2 or 3. The determined or supposed sizes of particles can be given as supplementary data. In many studies, however, the elutriation scale must be joined to the sieve scale and should have nearly the same size ratios between the grade limits as the latter. In his study of coastal plain gravels the writer used the following assumed hydraulic values for the continuation of the sieve grades:

²⁸ Richards, R. H., Textbook of Ore Dressing, p. 264, New York, 1909.

²⁹ Richards, R. H., *Op. cit.*, pp. 262-268.

Holmes, A., *Op. cit.*, p. 207.

Moles, E. C. Jul., Bulletin du Department de l' Agriculture aux Indes Neerlandaises, Buitenzorg, 1910, pp. 7-15.

³⁰ These values are given by Richards, *Op. cit.*, pp. 262-268, and by Holmes, *Op. cit.*, p. 206.

³¹ This subject is briefly and cogently discussed by Richards, *Op. cit.*, pp. 262-268.

Diameter	Millimeters per second
1/16	4
1/32	4/3
1/64	4/9
1/128	4/27

This scale has no precise theoretical justification but is a simple and easily remembered scale closely approximating the mean of several published tables by hydraulic values throughout its range.

PROCEDURE

The general plan of elutriation by settling consists of allowing the particles to settle for a fixed period of time from a thoroughly mixed turbid suspension; at the end of that time the water and those particles not settled are drawn off as rapidly as possible with a syphon of glass or rubber tube. The settled portion is remixed with fresh water and the operation repeated. It is apparent that while all the larger particles are settling from the top of the column that a half of those particles which settle only half as rapidly will settle out of the lower part of the column; i.e., all of these contained in the lower half column. If the grade scale be built on the ratio 3 in hydraulic values instead of 2, the progress of separation by settling will be shown on the following table.

TABLE SHOWING PROGRESS OF REMOVAL OF FINER GRADES BY WASHING⁸²

Grade limits mm. per second	Mean hydrau- lic value mm. per second	Per cent of grade present			
		After 1st. washing	After 2nd. washing	After 3rd washing	After 4th washing
27		100	100	100	100
	15.6	58	33	19	11
9		33	11	3.7	1.2
	15.2	19	3.7	.7	.1
3		11	1.2	.1	
	1.7	6.3	.4		
1		3.7	.1		

From the table it appears that after four washings of grade 81-27 mm. per second there will remain about 11 per cent of grains

⁸² Time of settling just permitting grains of value 27 to fall from top.

of mean size in the 27.9 mm. per second grade, only 1.2 per cent of the smallest grains but approaching 100 per cent of the largest grains. It is evident that complete removal of grains just under the lower limit of the grade being washed is not practicable and some slight contamination by these remains even after many washings. In most work three or four washings must suffice. Corrections based on the principle of the table above may be applied if the need justifies and manipulations have been sufficiently precise.

In the rising current type of elutriation a few minutes of operation will do the work of many washings, but here also the removal of grains just below the lower size limit of the grading being washed is relatively slow. The writer is not aware that rising current elutriations have been devised for very low velocities, such as those below 1/50 mm. per second except as attempted in the Yoder centrifugal elutriator.

DEFLOCCULATION³³

In analysing clays, important difficulties arise because of the presence of materials having colloidal properties and capable of forming aggregates under varying electrolytic conditions. In all analyses by elutriation it is desirable to use distilled water and reduce error due to flocculation to as low a value as possible. Water from condensed steam in a heating system or rain water is preferable to tap water where distilled water in the necessary quantities is not available. In analysing most clays treatment for deflocculation is necessary. For a description of methods the reader is referred to the work of Goldman,³⁴ Milner,³⁵ and Steiger.³⁶

Clays differ so widely one from another that it is difficult to give precise directions applicable to all. Probably the best general procedure is a deflocculation by shaking in a solution of sodium carbonate or ammonia and suspension for elutriation in a similar weakly alkaline solution. It is to be borne in mind that electrical energy must be supplied to bring about the electrical neutralization of the

³³ In writing and revising this section the writer has had the benefit of valuable suggestions and advice from M. S. Littlefield, of the University of Iowa, M. I. Goldman, of the U. S. Geol. Survey, and R. O. E. Davis, of the U. S. Bureau of Soils.

³⁴ Goldman, M. I., *The Petrography and Genesis of the Sediments of the Upper Cretaceous of Maryland*, pp. 115-119, Johns Hopkins Univ. Press, 1916.

³⁵ Milner, H. B., *An Introduction to Sedimentary Petrography*, p. 24, London, 1922.

³⁶ Steiger, Geo., *Treatise on Sedimentation*, Edited by W. H. Twenhofel, pp. 630-631, Baltimore, 1926. See also U. S. Bureau of Soils, *Bulletins* 24 and 84.

aggregated clay particles and effect deflocculation, and also that though the sizes of the aggregates may be materially reduced by such treatment complete deflocculation such that each subsiding particle is a single mineral grain is essentially impossible except by a precise treatment worked out by the student with particular reference to the physical and chemical condition of the sample in hand.

It is further necessary to emphasize that since all natural clays consist largely of colloidal material in varying degrees of flocculation and were such at the time of accumulation, it is futile to hope in most cases that conditions closely approaching those obtaining at the time of deposition can be set up by treatment for deflocculation or that the size distribution as determined by hydraulic methods can be used in the interpretation of the aqueous conditions of origin with confidence in those sediments fine enough to be materially affected by colloidal phenomena. The writer does not wish to convey the idea that it is useless to attempt to analyse fine grained sediments, but he does wish to emphasize the view that results obtained by a routine application of any single procedure to a variety of sediments are not likely to be of great significance or value in interpreting the origin of the material in question. It should be borne in mind that some sediments may have been in a highly flocculated condition at the time of deposition and that to attempt complete deflocculation as a general goal is as pernicious as the analysis of sediments without any deflocculation procedure.³⁷ It is to be hoped rather that each student will endeavor, by a study of the behavior of the sediment in hand under various electrolytic conditions and by a study of resulting particles under the microscope, to learn the nature of the existing state of aggregation and to adapt his treatment for deflocculation so as to convert the sediment most nearly into a significant previous condition of aggregation whether that requires complete deflocculation, or very little, or none at all.

COMPUTING AND PLOTTING

METHODS OF COMPUTING

The computing involved in mechanical analysis consists for the most part of simple percentage arithmetic. For most purposes it can be carried out with sufficient accuracy by means of a ten-inch slide rule. When a sample has been analysed in one stage it is com-

³⁷ Davis, R. O. E., *The Interpretation of Mechanical Analysis of Soils as affected by Soil Colloids*, Jour. Amer. Soc. Agronomy, Vol. 14, pp. 296-297, 1922.

monly the case that the total of the separate weights is slightly less than the weight of the total sample before analysis. With reasonable care the discrepancy can be kept down to a fraction of one per cent, even on light samples of but a few grams. The loss may be from any of the grades by lodgement in the sieves or otherwise. It is the custom among some workers to consider that the entire loss is from the fine grade. Unless this has been proven to be the case by careful tests, it seems better as a general practice to distribute the error among all the grades. This is accomplished by using the total resulting by addition of the separate weights rather than the original one.

In computing the percentages by slide rule slight errors of manipulation and reading will enter, causing the total of the percentages to add to less or more than 100. Here the discrepancy need be no more than one or two tenths of one per cent and it is the writer's custom to compute the largest percentage last and by adding the column of tenths of the other percentages determine the proper digit to be read in the tenths of the last and largest percentage. This should rarely differ from that actually appearing on the rule by more than .2 per cent. The result is then set down and checked by addition of the total to 100 per cent. Arithmetic or logarithmic methods can be applied similarly. The schedule given below is for the purpose of making more clear the methods of computing and also to summarize the procedure of one of the more complicated multi-stage analyses.

Total weight of sample = 13.79 kg.

Sieve grades	Weight	
+64 mm., separate washed	1.32 kg.	
+32 " " "	2.61 "	
+16 " " "	1.76 "	
Total	5.69 kg.	13.79 kg.
		5.69 "

—16 m., total weight (Too sticky for sifting) 8.10 kg.

Dried, mixed, quartered down

total weight used 4.17 kg.

Small quantity shaken over 1/16 mm. sieve to secure about 10 grams of normal —1/16 grade. Rest returned and total of close to 4.17 grams washed in jar with hose to

take out bulk of $-1/32$ grades. Residue then dried and sifted.

Sieve grades	Weight
+8 mm. separate	.73 kg.
+4 " "	.54 "
+2 " "	.48 "
Total	1.75 kg.
	Weight
	4.16 total -16 mm.
	1.75 total $16-2$ mm.

Total -2 grade 2.42 kg.

This residue of 2.42 kg. was quartered down to 47.31 grams and sifted.

Sieve grades	Weight
+1. mm., separate	10.31 gm.
+1/2 " "	11.73 "
+1/4 " "	6.30 "
+1/8 " "	4.29 "
+1/16 " "	3.89 "
	36.52 gm.
	47.31 gm. total -2 mm.
	36.52 " " $2-1/16$ mm.

10.79 gm. total $-1/16$ mm.

Then $-1/16$ remaining is less than the total amount by amount of that washed out. Some of the material originally saved from the -16 grade above is used for the elutriation.

Settling grades.

4/3 mm. per sec. separate	1.83 gm.
4/9 " " " "	1.64 "
4/27 " " " "	.89 "
-4/27 " " " "	.15 "

Total 4.15 gm.

Computation usually performed by slide rule.

Total sample of 13.79 kg.	= 100%	
then +64 " of 1.32 "		= 9.6%
+32 " of 2.61 "		= 18.9%
+16 " of 1.76 "		= 12.8%
-16 " of 8.10 "	= 58.7%	
Total -16 " of 4.17 "	= 58.7%	
then +8 " of .73 "		= 10.3%
+4 " of .54 "		= 7.6%
+2 " of .48 "		= 6.8%
-2 " of 2.42 "	= 34.0%	
Total -2 " of 47.31 gm.	= 34.0%	
then +1 " of 10.31 "		= 7.4%
+1/2 " of 11.73 "		= 8.4%
+1/4 " of 6.30 "		= 4.5%
+1/8 " of 4.29 "		= .13%
+1/16 " of 3.89 "		= 2.8%
-1/16 " of 10.79 "	= 7.8%	
Total -1/16 sample of 4.51 gm.	= 7.8%	
then +4/3 mm. sec. sample of 1.83 gm.		= 3.2%
+4/9 " " " of 1.64 "		= 2.8%
+4/27 " " " of .89 "		= 1.5%
-4/27 " " " of .15 "		= .3%
Check		100.0%

CHOICE OF PLOTTING SCALES

When the grade scale has been decided upon and the analyses made and computed there still remain a variety of forms in which the results may be presented. If a graphic form is chosen, whether pyramidal or cumulative as described below, choice must be made in either case whether the coarse grades shall be at the left or at the right of the diagram and what ratio shall obtain between the vertical percentage scale and the horizontal grade scale. A large number of different conventions have been used in the past with the result that direct comparison between the results obtained by different students has been impossible.³⁸ The great diversity which can be developed

³⁸ Goldman, M. I., *Petrography and Genesis of the Sediments of the Upper Cretaceous of Maryland*, pp. 169-170, Baltimore, 1916.

Woodford, A. O., *The San Onofre Breccia*, Univ. of Calif., Publications, Bull. of the Dept. of Geol. Sciences, Vol. 15, No. 7, p. 175, 1925.

Holmes, A., *Petrographic Methods and Calculations*, pp. 217-225, London, 1921.

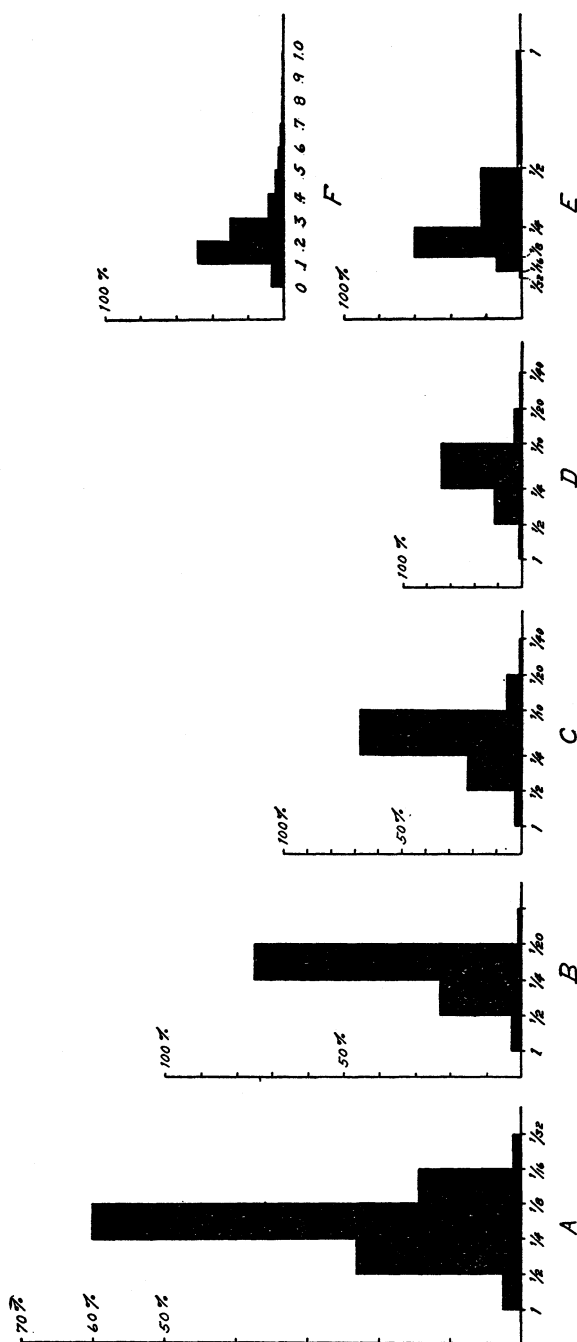


Fig. 3. Composition histograms for the same sediment made and plotted to six different scales, all of which have been used and published. The variation beyond the limits of recognition is apparent.

in the composition diagram of a given sediment by the use of different grade scales and plotting conventions is shown in Figure 3. Plotting with the coarse grades at the left has seemed to be most convenient and the card shown in Figure 4 is used in the sedimentation laboratory at the University of Iowa. The grade scale spaces on this card are made to conform with vertical spacing of a typewriter so

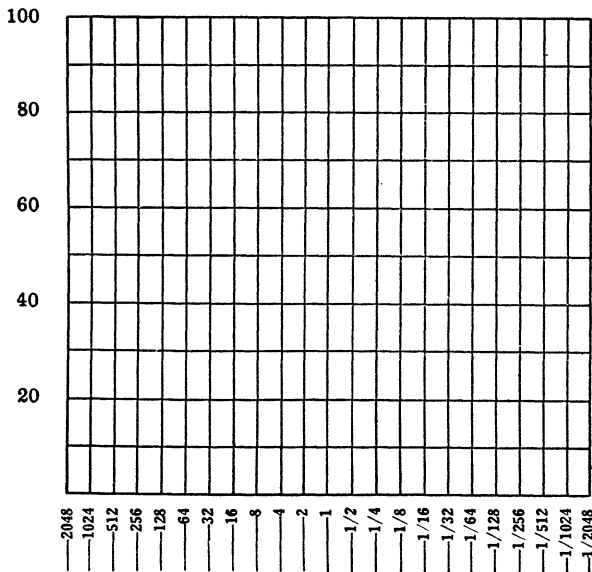


Fig. 4. Form card used in plotting histograms to the 1-2-4-8 mm. scale at the University of Iowa.

that the percentages may be filled in on a machine if desired. The ratio between vertical and horizontal scales is such that 100 per cent is equal to 20 grades of the ratio 2. By the use of such a card for plotting all analyses as a laboratory record the diagrams are immediately available in any combination or arrangement without re-drawing for reproduction by zinc etching and much time is saved in publication. The scale of reproduction can be varied somewhat without interfering greatly with comparison provided the ratio between vertical and horizontal scale is maintained constant.

Baker, H. A., *Geol. Magazine*, pp. 411-420, 463-467, 1920.

Dake, C. L., *The Problem of the St. Peter Sandstone*, Missouri School of Mines Bulletin, Vol. VI, No. 1, Plates V-XII, incl., 1921.

Trowbridge, A. C., and Mortimore, M. E., *Correlation of Oil Sands of Sedimentary Analysis*, *Economic Geology*, Vol. XX, No. 5, p. 417, 1925.

DISTRIBUTION AND CUMULATIVE DIAGRAMS

Two types of diagrams are in current use and both have good claims for recognition. The distribution pyramid shown in Figure 5 has the advantage that it is a strict presentation of numerical facts.

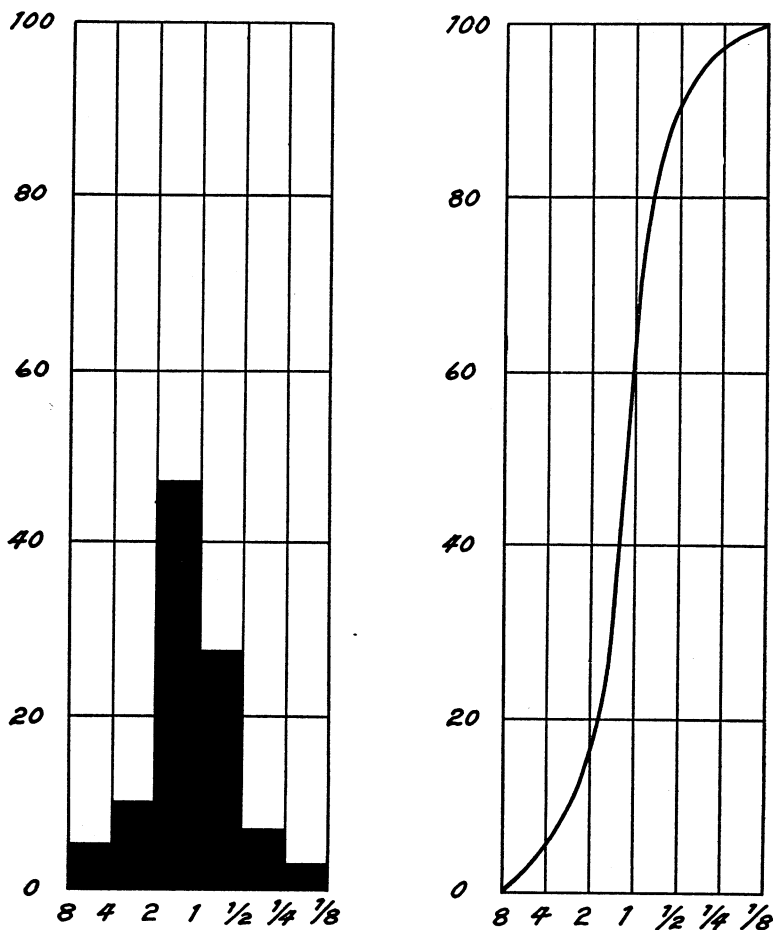


Fig. 5. Histogram and cumulative curve for the same composition.

There is no element of interpretation in it. It is probably more readily visualized by persons unaccustomed to either than is the cumulative diagram. The latter diagram is partially interpretative in the drawing of the smoothed curve and permits the presentation of several diagrams in one plot. It also permits the plotting of analyses made to different grade scales on the same diagram more

readily. It seems that each type of scale has its own advantages and that both may sometimes be needed to convey most effectively this type of data.

TRANSFORMATION OF GRADE SCALES

Analyses made to any grade scale may be plotted on the cards shown in Figure 4 directly in the pyramidal form by drawing inter-

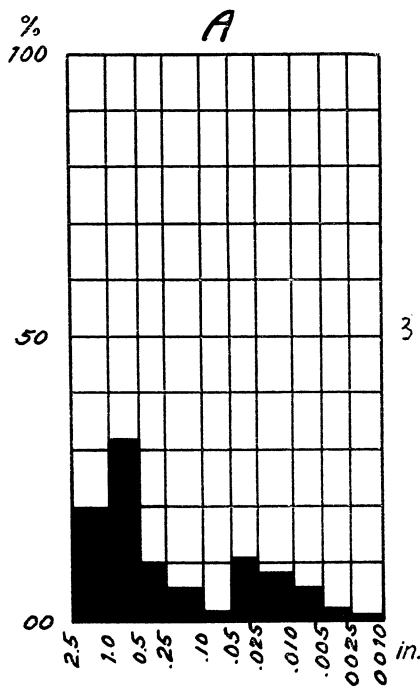


Fig. 6A. Histogram of original analysis.

mediate vertical lines at the abscissæ points of the new grade scale and filling in the new columns thus made. The comparison of such diagrams with those made to the normal grade scale is difficult unless the two are very closely juxtaposed and it is preferable to transform the analysis in question to the standard grade scale. This is done by plotting the analysis in the cumulative form and drawing a smooth curve through the fixed points. Ordinates may now be read on the curve for the abscissæ points of the standard grade scale and the pyramid plotted for these values as read. (Figure 6.) Similar methods may be used for constructing a pyramidal diagram of smaller grade ratios, Figure 6-D. No more information is added

in such transformation and the result is slightly less accurate than the fundamental pyramid of the grade scale of analysis but the form may be more favorable for interpretation.³⁹

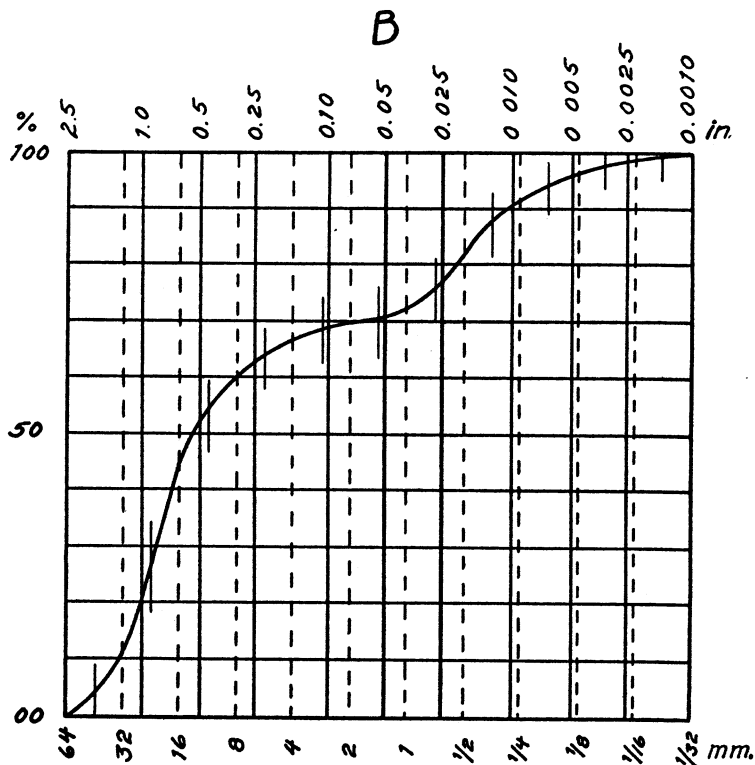


Fig. 6B. Cumulative curve used in reading ordinates at abscissæ points of desired scales.

³⁹ This paper is to be followed by another consisting of a graphic compilation of several hundred mechanical compositions of modern sediments for comparison and reference.

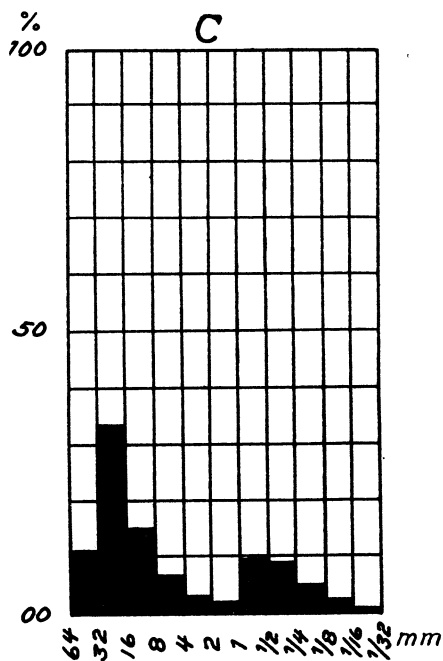


Fig. 6C. Histogram of same data transformed 1-2-4-8 mm. scale.

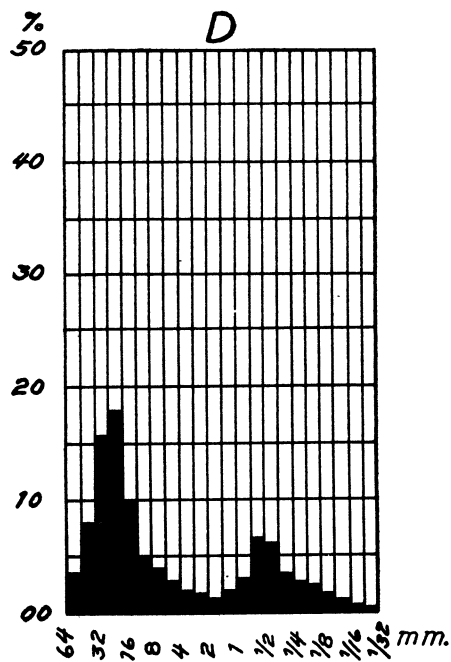


Fig. 6D. The same plotted to twice the number of grades, i.e., ratio of the square root of 2.

QH
1
I 642
NEW SERIES No. 120

DECEMBER 1, 1926

UNIVERSITY OF IOWA STUDIES

STUDIES IN NATURAL HISTORY

VOLUME XI

NUMBER 12

AN ECOLOGICAL STUDY OF THE FISHES OF THE LAKE OKOBOJI REGION

by

AUSTIN P. LARRABEE

PUBLISHED BY THE UNIVERSITY, IOWA CITY, IOWA

Issued semi-monthly throughout the year. Entered at the post office at Iowa City, Iowa,
as second class matter under the Act of October 3, 1917

UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

VOLUME XI

NUMBER 12

AN ECOLOGICAL STUDY OF THE FISHES OF THE LAKE OKOBOJI REGION

by

AUSTIN P. LARRABEE

PUBLISHED BY THE UNIVERSITY, IOWA CITY, IOWA

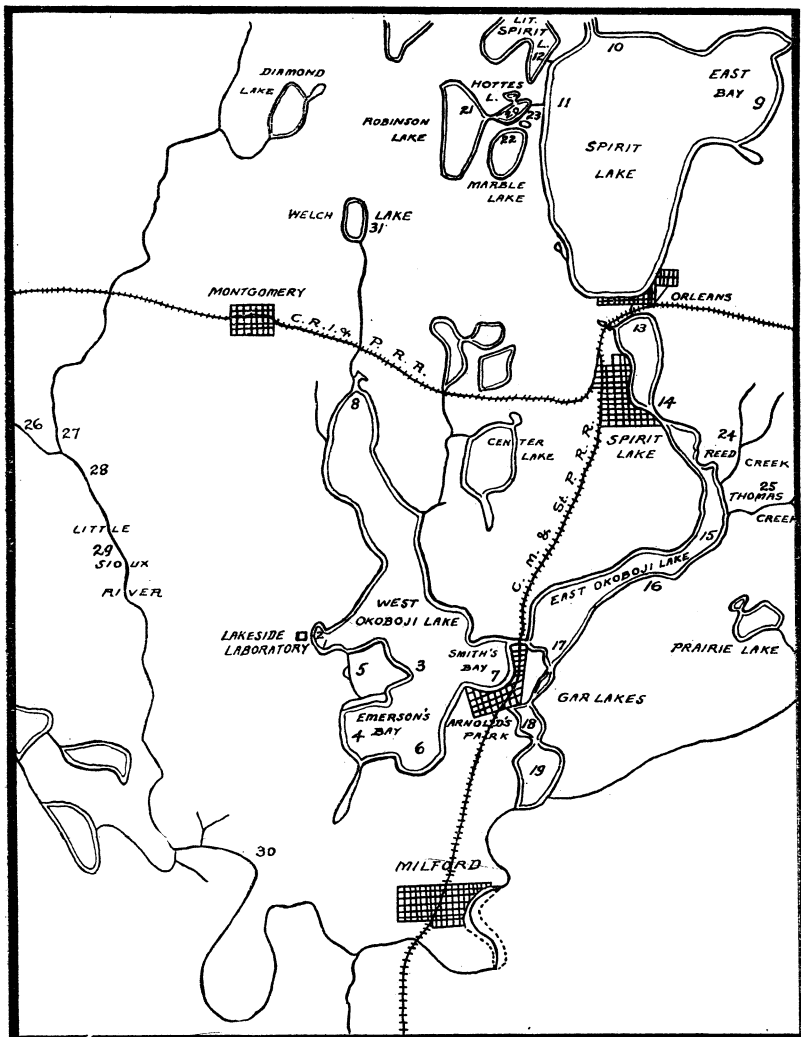


Fig. 1. Map of the Lake Okoboji Region, showing collecting stations

- | | |
|---------------------------|---------------------------------|
| 1-8. West Okoboji Lake | 18. Middle Gar Lake |
| 1. Miller's Bay | 19. Lower Gar Lake |
| 2. Sand-bar | 20. Hottes Lake |
| 3. Gull Point | 21. Robinson Lake |
| 4. Emerson's Bay | 22. Marble Lake |
| 5. Drainage Canal | 23. Sunken Lake |
| 6. Deep Hole, Emerson Bay | 24. Reed Creek |
| 7. Smith's Bay | 25. Thomas Creek |
| 8. North End | 26-30. Little Sioux River |
| 9-11. Spirit Lake | 26. West Branch |
| 9. East Bay | 27. East Branch |
| 10. Crandall's Lodge | 28. Below junction of 26 and 27 |
| 11. Opposite Hottes Lake | 29. Near Hanging Bog |
| 12. Little Spirit Lake | 30. Big Bend |
| 13-17. East Okoboji Lake | 31. Welch Lake |
| 13. Outlet of Spirit Lake | |
| 14. Drawbridge | |
| 15. Kline's Bay | |
| 16. Rocky Point | |
| 17. Outlet | |

U. S. Bureau of Fisheries
U. S. Fish Commission
5-21-1932

AN ECOLOGICAL STUDY OF THE FISHES OF THE LAKE OKOBOJI REGION

INTRODUCTION

This paper contains the results of studies of the fishes of the Lake Okoboji region, made by the writer during the summers of 1921, 1922, 1924, and 1925. The writer spent in all thirty-five weeks at the Lakeside Laboratory while carrying on this work. At first the intention was to investigate the distribution of certain fishes in the lakes with the factors involved, but this was enlarged later to include the listing of all the fishes found there together with their ecological habitats. The paper includes the studies not only of lake fishes but also of certain creek fishes and those of the Little Sioux River.

Through the courtesy of the Iowa State Fish and Game Department, the writer was allowed to collect the fishes necessary for this study. For this purpose seines were commonly used, and at times the hook and line. This was supplemented, when there was opportunity, by the examination of fishes in live bait boxes and in the catches of the local fishermen, together with such information as could be obtained regarding fishes. The location of the various collecting stations is shown in Figure 1, a map of the region. At the time of collecting, notebook records were made of the time of day, temperature, and weather conditions, as well as data regarding the different species and the numbers of each taken. The fish for identification were kept alive if possible. Others were preserved in 10% formalin. In case the food of the fish was to be determined, the body cavity was opened so as to allow the preservative free access to the digestive tract. This examination was made at the laboratory as soon as possible after collecting. The fish was first measured and the length, which did not include the caudal fin, recorded. Then the stomach and intestines were removed, slit open, and the contents carefully scraped out on a glass slide. The materials were examined mainly under a dissecting microscope, using the compound microscope when necessary. The different constituents were then teased apart and segregated with needles and the percentage of the volume of each estimated.

But little work has been done with the fishes of this region. Meek collected here in 1890 and records eighteen species from Spirit, East, and West Okoboji Lakes.¹ Everman also visited Spirit Lake in 1892. The statements made in his itinerary are brief and concise.

“Nov. 1. Went to Spirit Lake, Iowa.

“Nov. 2. Cold weather having set in, we decided to close the work here and return to Washington.”²

Although his stay was brief, he found one of the eighteen species recorded by Meek. More recently, in October, 1920, Mr. Carfield, Superintendent of Fish Culture of the U. S. Biological Station at Fairport, Iowa, visited the lakes, making an investigation of the conditions affecting the supply of fishes, especially of the game fishes.

In a letter to Mr. W. A. Albert, State Fish and Game Warden, he casually mentions fourteen species occurring in the lakes. These are referred to by their common names, making exact identification often difficult or impossible. However, three new species are added to Meek's list. One of them, the common carp, *Cyprinus carpio*, was introduced into the lakes after Meek and Evermann were there. The other two, the channel cat, *Ictalurus punctatus*, and the white bass, *Roccus chrysops*, are probably native but have had their original numbers increased through stocking by the State Department.

The writer wishes to express his indebtedness to Dr. F. A. Stromsten for the advice given and suggestions made during the progress of this study and in the preparation of the manuscript. His friendly interest has been an invaluable aid throughout. The writer is indebted also to Mr. W. A. Albert, State Fish and Game Warden, for permission to collect fishes and for information given, and to the U. S. Fish Commission for literature supplied. He owes much to Mr. Will Shear, Warden in charge of the Fish Hatchery at Orleans, and to Mr. Frank P. Hopkins of Spirit Lake for assistance freely and willingly given. Their knowledge of the fishes and of their haunts has been of great value in making this study. He is indebted, also, to Mr. Harry Tennant for his courtesy in allowing the writer free access to his mounted specimens of fishes and for information given. And for aid in collecting and in other ways, the

¹ Meek, S. E. Notes on the Fishes of Western Iowa and Eastern Nebraska. Bull. U. S. F. C., Vol. 14, p. 133-138, 1894.

² Evermann, B. W. and Cox, U. O. Report on the Fishes of the Missouri River Basin. Rep. U. S. Comm. of Fish and Fisheries, p. 352-429, 1894.

writer expresses his appreciation to Professors H. M. Kelly and Albert Kuntz, and to Messrs. E. M. Fitch, J. W. Breukelman, G. E. Potter, and D. T. Jones. To all these as well as to others unnamed, the writer wishes to record his thanks.

LIST AND CLASSIFICATION OF THE FISHES OF THE LAKE OKOBOJI REGION

The following is a systematic outline of the fishes recorded from this region. But one sub-class, the Teleostomi, of the class Pisces, the true fishes, is concerned. Seven orders of this sub-class are represented here. The classification employed is based on that of Jordan and Evermann with the adoption of certain changes made by Jordan in his recent work on fishes.³ The species recorded by Meek are indicated by a letter M after them. If a species has not been observed by the author, it is bracketed.

Series Ganoidea.

Order Selachostomi. The Paddlefishes.

Family Polyodontidæ. The Paddlefishes.

Polyodon spathula (Walbaum). Spoonbill.

Order Rhomboganoidea. The Garpikes.

Family Lepidosteidæ. The Garpikes.

Lepidosteus osseus (Linnæus). Long-nosed Gar. M.

Lepidosteus platystomus (Rafinesque). Short-nosed Gar.

Series Teleostei.

Order Isospondyli.

Family Hiodontidæ. The Mooneyes.

Hiodon alosoides (Rafinesque). Northern Mooneye.

Family Salmonidæ. The Salmon Family.

Cristivomer namaycush (Walbaum). Great Lake Trout.

Order Eventognathi.

Family Catostomidæ. The Suckers.

Ictiobus cyprinella (Cuvier & Valenciennes). Big-mouth Buffalo.

Ictiobus bubalus (Rafinesque). Small-mouth Buffalo.

Carpionodes carpio (Rafinesque). Common River Carp.

Catostomus commersonii (Lacepede). Common Sucker.⁴

Moxostoma aureolum (Le Sueur). Common Red-horse.

³ Jordan, D. S. Fishes. D. Appleton & Co., N. Y., 1925.

⁴ Another sucker, *C. nigricans* probably, has been reported to the author who has not been able to verify the report.

Family Cyprinidæ. The Minnow Family.

Cyprinus carpio Linnæus. Common Carp.*Hybognathus nuchalis* Agassiz. Silvery Minnow.*Pimephales notatus* (Rafinesque). Blunt-nosed Minnow.*Semotilus atromaculatus* (Mitchill). Horned Dace.*Abramis crysoleucas*. (Mitchill). Golden Shiner. M.*Cliola vigilax* (Baird & Girard). Bullhead Minnow.*Notropis cayuga* Meek. Cayuga Minnow.*Notropis heterodon* (Cope). Variable-toothed Minnow.*Notropis blennioides* (Girard). Straw-colored Minnow.*Notropis hudsonius* (De Witt Clinton). Shiner. M.*Notropis lutrensis* (Baird & Girard). Red-finned Minnow.*Notropis jejunus* (Forbes). Shiner.*Rhinichthys atronaso* (Mitchill). Black-nosed Dace.*Hybopsis storerianus* (Kirtland). Storer's Chub.

Order Nematognathi. The Catfishes.

Family Siluridæ. The Catfishes and Bullheads.

Ictalurus punctatus (Rafinesque). Channel Cat.*Ameiurus natalis* (Le Sueur). Yellow Bullhead.*Ameiurus nebulosus* (Le Sueur). Speckled or Brown Bullhead.*Ameiurus melas* (Rafinesque). Black Bullhead.*(Leptops olivaris* Rafinesque. Flat-head Cat.)

Order Haplomi.

Family Esocidæ. The Pikes and Pickerels.

Esox lucius Linnæus. Common Pike. M.

Family Pœciliidæ. The Killifishes.

Fundulus diaphanus menona (Jordan & Copeland). Menona Top-minnow.*(Fundulus zebrinus* Jordan & Gilbert. M.)⁵

Order Acanthopteri. The Spiny-rayed Fishes.

Family Gasterosteidæ. The Sticklebacks.

Eucalia inconstans (Kirkland). Brook Stickleback.

Family Percopsidæ. The Trout-perches.

Percopsis guttatus Agassiz. Trout-perch. M.

Family Centrarchidæ. The Sunfishes.

Pomoxis annularis Rafinesque. White Crappie.*Pomoxis sparoides* (Lacepede). Black Crappie. M.*Ambloplites rupestris* (Rafinesque). Rock Bass.⁵ For discussion of this record, see page 15.

- Apomotis cyanellus* (Rafinesque). Green Sunfish.
Lepomis megalotis (Rafinesque). Long-eared Sunfish.
Lepomis humilis (Girard). Orange-spotted Sunfish.
Lepomis pallidus (Mitchill). Bluegill. M.
Eupomotis gibbosus (Linnæus). Common Sunfish. M.
(*Micropterus dolomieu* Lacepede. Small-mouthed Black Bass. M.)
Micropterus salmoides (Lacepede). Large-mouthed Black Bass. M.

Family Percidæ. The Perch Family.

- Stizostedion vitreum* (Mitchill). Wall-eyed Pike. M.
Stizostedion canadense griseum (De Kay). Sauger. M.
Perca flavescens (Mitchill). Perch. M.
Percina caprodes (Rafinesque). Log-perch.
Boleosoma nigrum (Rafinesque). Johnny Darter. M.
Etheostoma iowæ Jordan & Meek. Iowa Darter. M.

Family Serranidæ. The Sea Bass.

- Roccus chrysops* (Rafinesque). White Bass.

Family Sciaenidæ. The Drums or Croakers.

- Aplodinotus grunniens* Rafinesque. Sheepshead.

HABITAT AND DISTRIBUTION

Polyodon spathula (Walbaum). Spoonbill; Paddlefish

No specimens of the spoonbill have been taken by the writer. Several large-sized ones, however, have been taken during the past twelve or fifteen years in East and West Okoboji Lakes. These have been taken mainly during the fall and winter months. An extremely large one, and the largest one yet recorded, as given in the Okoboji Protective Association Bulletin, No. 12, 1916, measured six feet and nine inches in length,⁶ and weighed 185 pounds. This individual, a male, was speared by a fisherman, R. Vandergeek, through the ice near the north end of West Okoboji Lake in the winter of 1915-1916. The same article relates the capture of another one, also speared through the ice, off Pillsbury's Point in the same lake. This one, which was a female, is reported to have weighed 210 pounds and to have measured six feet and seven inches from tip to tip. The author has found on investigation that the weight of the latter paddlefish was exaggerated. Mr. Hopkins, in a letter to

⁶ Measurements are from tip to tip.

the author writes, "——it weighed, when Mr. Tennant received it, 168 pounds and had been out of the water a week. Mr. Tennant estimated its weight not over 175 pounds when speared." This specimen and a third one were mounted by, and are in the possession of Mr. Tennant who has given the writer the opportunity of examining them. The third paddlefish, which was caught in a gill net in Miller's Bay in January, 1918, measured six feet and four inches over all and weighed 146 pounds. At least five other large-sized ones, although considerably smaller than those discussed, have been taken in East or West Okoboji Lakes. But none have been taken since 1918 although certain fishermen have reported that they have seen others.

It seems probable that very few if any spoonbills still exist in the lakes, and that the number has been limited in the past. The species is one of rivers and larger streams rather than of lakes, occurring in waters with muddy bottoms. Yet it is in the lakes that the largest individuals have been found. Evermann and Clark record two from Lake Manitou, Indiana, weighing 173 and 163 pounds respectively.⁷ Forbes and Richardson mention another large specimen from Lake Tippecanoe, Indiana, which weighed 150 pounds.⁸ Similar examples from other lakes are on record. The large size attained in the lakes may be due in large measure to the favorable food conditions found there. For the lakes furnish for this species an especially abundant supply of food which consists largely of entomostraca and insect larvæ.

Lepidosteus osseus (Linnæus). Long-nosed Gar

This species is reported by Messrs. Hopkins and Shear to be commonly distributed in the three major lakes of this region. But few have been taken with seine during the summer. These were seined over both muddy and sandy bottoms. Apparently this species prefers deeper water in the summer than the Short-nosed Gar. Otherwise the two resemble each other closely in their habits and distribution.

Lepidosteus platystomus (Rafinesque). Short-nosed Gar

This fish occurs commonly in waters of shallow to moderate depths, mainly among aquatic vegetation and over both muddy and sandy bottom. Both this and the preceding species have the habit of

⁷ Evermann and Clark, Lake Maxinkuckee, p. 310.

⁸ Forbes and Richardson, Fishes of Illinois, p. 17.

floating on the surface for some time, resembling a stick in the water. This may be of some value in catching their prey, although none have been observed to feed at such times. The jaws armed with sharp teeth are well fitted for seizing and holding their prey. Mr. G. E. Potter found the food of the adults here to consist of about 60% fish and 40% crayfish.⁹

Hiodon alosoides (Rafinesque). Northern Mooneye

This species is of rare occurrence in the lakes. The writer has taken none and has learned of but two specimens being taken. One of these was caught in East Okoboji Lake in August, 1922. This specimen was not seen by the writer but a plaster mold of it made by a storekeeper in Orleans was examined. The diagnostic character of the species, the dorsal fin with nine rays and placed slightly posterior to the ventral one, was clearly evident in the imprint.

The other specimen was caught several years ago in Minnewashta Lake, the Middle Gar Lake. It was mounted and kept as a curiosity by a storekeeper in Arnold's Park. Here, in the summer of 1925, the writer had the opportunity of examining and identifying it.

Cristivomer namaycush (Walbaum). Great Lake Trout

This trout is not a native here, and although several attempts to introduce it have been made during the past twenty-five years, it probably exists now in limited numbers if at all. It has been introduced into both Spirit and West Okoboji Lakes, mainly in the latter. In 1922, the latest attempt, 40,000 adult trout were planted in West Okoboji Lake. On the whole, these different attempts have not been successful. About fifteen years ago four or five trout were caught. One of these taken in Spirit Lake was mounted and in the summer of 1925, still hung on the wall of a pool room in the town of Spirit Lake. No others have been taken so far as the writer could learn.

The Great Lake trout in general requires deep cold water, apparently able to exist under such conditions with a relatively small amount of oxygen.¹⁰ Spirit Lake, which has a maximum depth of 7.6 m. and only a slight change in temperature from the surface to the bottom, evidently furnished unfavorable conditions for this fish. Successful planting could not be expected here. West Okoboji Lake

⁹ Potter, G. E., The Food of the Short-nosed Garpike (*Lepidosteus platystomus*). Ia. Acad. Sci., Vol. XXX, p. 167-170, 1923.

¹⁰ Kemmerer, George, Bouvard, J. F., and Boorman, W. R. Northwestern Lakes of the U. S. Biological and chemical studies with reference to the possibilities in production of fish. Bull. Bur. of Fisheries, Vol. 39, p. 51-140, 1923-24.

with a maximum dept of 40.2 m. has both the depth and the low temperature required. After the summer stratification has taken place, the lowest stratum, the hypolimnion, remains practically uniform in temperature, but not so in its oxygen content. The sources of oxygen are cut off, for the hypolimnion is cut off from the air by the upper two layers and there is little or no photosynthesis. On the other hand, through decomposition and respiration the amount of oxygen is decreased. Birge and Juday, on July 31, 1919, found a decrease from 2.23 cc. per liter at 15 m., with a slight increase at 18 m., to 0.86 cc. at 33 m. From their results, they state, "—— it is safe to predict that this gas all disappeared, from the lower portions of the hypolimnion at least, before the time of the autumnal overturn."¹¹ Students of Stromsten have found such to be the case, and the amount of oxygen decreased in the upper hypolimnion so as to make conditions unfavorable for the trout. Again the food supply, largely of fish, may be limited in the depths which the trout would occupy in summer. The author has no evidence, however, to support this.

Ictiobus cyprinella (Cuvier & Valenciennes). Big-mouth Buffalo

This is the common buffalo fish of the lakes, occurring in the three major lakes and in the smaller ones adjoining Spirit. During the summer it prefers weedy waters six to eight meters deep over a mud bottom, although the writer has taken three specimens in East Okoboji at the depth of two to three meters. During the spawning season in the spring, buffalos are said to be tolerably common in the shallow water along the shores where the eggs are deposited.

Ictiobus bubalus (Rafinesque). Small-mouth Buffalo

Meek records this species, reporting two or three specimens taken in East Okoboji. The author has taken none. It is reported from all three major lakes, occurring in much less numbers than the preceding species.

Carpiodes carpio (Rafinesque). Common River Carp

This species has not been taken in any of the lakes, but occurs tolerably commonly in the Little Sioux River where it was seined by the author. It was taken most commonly in the swifter waters of the West Branch, and in limited numbers only below the junction of the two branches where the flow was less rapid.

¹¹ Birge, E. A. and Juday, C. A Limnological Reconnaissance of West Okoboji. Stud. in Nat. Hist., Univ. of Ia., IX, No. 1, p. 42, 1920.

Catostomus commersonii (Lacepede). Common Sucker

The common sucker occurs commonly in the major lakes and in the Gar Lakes. In the summertime, it is found in the deeper waters mainly on a rocky bottom, and has not been taken with the seine along shore. It is also tolerably common in the Little Sioux River, showing a preference for the swifter flowing portions.

Moxostoma aureolum (Le Sueur). Red-horse

The writer has not taken any of this species in the lakes. Two specimens, one a mounted specimen taken by Mr. Tennant in East Okoboji and the other taken in West Okoboji by Mr. Hopkins, have been examined. It is said by Mr. Tennant to occur in the Gar Lakes also. One was seined by the writer in the West branch of the Little Sioux River. Judging from the statement made to the writer, it is evidently an uncommon fish in this region.

Cyprinus carpio Linnæus. Carp

The carp first appeared in the lakes fifteen or sixteen years ago, and in a few years it was common in East and West Okoboji and in the Gar Lakes. High water, five or six years later, enabled it to extend its range into Spirit Lake where it occurs in lesser numbers than in the other lakes mentioned. It prefers weedy muddy bottomed portions of the lakes in shallow to moderate depths.

In the Little Sioux River two specimens of the variety known as the mirror carp were taken in July, 1922. In this variety the scales are few and much enlarged occurring in two or three irregular rows of scales, with the rest of the body naked. None of these have been taken in the lakes.

Hybognathus nuchalis Agassiz. Silvery Minnow; River Shiner

This minnow, as the second name infers, is a river form, occurring abundantly in the Little Sioux mainly over a muddy bottom. None have been recorded from any of the lakes. It is used to some extent for commercial bait, but the distance to the river makes it too inconvenient to be commonly used.

Pimephales notatus (Rafinesque). Blunt-nosed Minnow; Chub

The blunt-nosed minnow prefers weedy shallow waters with muddy bottom. The writer found it common in North Hottes Lake but did not take any elsewhere except in the Little Sioux River, although it was reported by Mr. Shear to be common in both Spirit and East Okoboji Lakes.

This and the bullhead minnow, *Chiola vigilax*, are the ones most commonly used for bait by the fishermen at the lakes. These two resemble each other so closely that they are not commonly distinguished as separate species. Besides the generic differences of the two, *notatus* has a blunter nose and the scales on the upper half of the body are dark-edged due to the concentration of the minute dots there. *Vigilax*, on the other hand, has a more rounded nose, and the specks are scattered over the scales rather than restricted to the edges.

Semotilus atromaculatus (Mitchill). Horned Dace; Creek Chub

This is a typical creek fish, occurring commonly in both Reed and Thomas Creeks. This is one of the pioneer fishes to take possession of young brooks or creeks. It is found especially in the deeper pools under shelving banks or tree roots where the current is strong enough to keep the water clean and well oxygenated.

Abramis crysoleucas (Mitchill). Golden Shiner

The golden shiner was taken from the three major lakes and from Marble, Hottes, and Robinson Lakes. It was found most common in the three last lakes, showing a preference for weedy and comparatively shallow water with muddy bottom. In East Okoboji and Spirit Lakes, a limited number was taken over a sandy bottom.

Chiola vigilax (Baird & Girard). Bullhead Minnow

But two specimens of this minnow were taken by the writer in the major lakes. One of these was seined in Miller's Bay, West Okoboji Lake, the other near Crandall's Lodge at the north end of Spirit Lake. Both were taken near patches of weeds, over a sandy or gravelly bottom. Such isolated occurrences suggest the possibility that these had escaped from the bait boxes of local fishermen. The writer has seined it in large numbers in Welch Lake, and it is reported by Mr. Hopkins to be as common in Center Lake. In Welch Lake it was taken in shallow water over a muddy bottom comparatively free of water plants.

Notropis cayuga Meek. Cayuga Minnow

This is an uncommon minnow in this region, and was taken in three localities only, Miller's Bay, (West Okoboji Lake), Hottes Lake, and Sunken Lake. In the first two it was taken in shallow water between the water weeds and the shore and over sandy bottom. But in Sunken Lake where it occurred rather commonly, it

was found among a dense growth of aquatic vegetation, mainly *Elodea*, and over a muddy bottom.

Notropis heterodon (Cope). Variable-tooth Minnow

This minnow is, in general, rare in the lakes. In a kettle hole near Stony Point, East Okoboji, it was found tolerably common. Here it was taken among weeds over a bottom of sandy silt. Otherwise it was not taken except in Miller's Bay where a half dozen in all were seined. The conditions were the same as those given for *cayuga*.

These two minnows, *heterodon* and *cayuga*, resemble each other closely. The latter has a very small mouth and a pale chin, while the former has a moderate sized mouth and a black chin.

Notropis blennioides (Girard). Straw-colored Minnow

This species is common in the Little Sioux River, and occurs in limited numbers in West Okoboji Lake and in Reed and Thomas Creeks. It has not been seined in any other of the lakes, but probably occurs in East Okoboji at least. Apparently it prefers the cool running waters of streams. In West Okoboji it was taken in shallow water along shore over a sandy bottom.

Notropis hudsonius (De Witt Clinton). Shiner; Spot-tailed Minnow

This is the most common minnow of the major lakes. None were taken in any of the minor ones. It frequents shallow water along shore generally over a sandy or gravelly bottom. Although still common, the numbers have been reduced by its use for live bait. Meek, in 1892, found it the principal minnow used for this purpose by the local fishermen.¹² That it is not the principal one now is due to its lessened numbers, and because other species of minnows can be more easily obtained in some of the nearby smaller lakes.

Notropis lutrensis (Baird & Girard). Red-finned Minnow

This minnow is a river dweller occurring rather commonly in the Little Sioux River. It shows a preference for the swift water of the riffles of the river. Two specimens only have been taken in the lakes. One of these was taken by Mr. Hopkins from the East Lake in July, 1922. The second one was seined by Messrs. Jones and Breukelman in Miller's Bay in July, 1924. It seems probable that

¹² Meek, Seth E. Fishes of Western Iowa and Eastern Nebraska, p. 136.

these two had escaped from minnow boxes, rather than occurring naturally in the lakes.

Notropis jejunus (Forbes). Shiner; Gull Point Chub

This shiner is apparently a localized form occurring mainly around Gull Point, West Okoboji Lake, thereby giving it the name of Gull Point Chub. But one specimen was taken by the writer. This was seined August 4, 1922, in clear shallow water over a sandy bottom.

Rhinichthys atronasmus (Mitchill). Black-nosed Dace

The black-nosed dace, like the horned dace, is a typical creek fish and is found tolerably common under similar conditions in Reed and Thomas Creeks. It has not been found elsewhere in this region.

Hybopsis storerianus (Kirtland). Storer's Chub; River Chub

The writer has seen but one specimen of this species, this one caught by Mr. Hopkins in East Okoboji Lake. Mr. Shear states that it is common in the Little Sioux River and is taken occasionally in the lakes during the spring seining.

Ictalurus punctatus (Rafinesque). Channel Cat

The channel cat is undoubtedly a native of this region as specimens have been taken in the Little Sioux River. Mr. Shear informed the writer that this species was introduced into the lakes about 1913 or 1914. In the winter of 1917-18, eighteen of these and the flathead cats, averaging sixteen pounds in weight, were taken in gill nets. Small fry of this and the other large cat-fish were first seen in the summer of 1921. In 1922, the State Fish and Game Department introduced 30,000 adults into West Okoboji and 18,000 in Spirit Lake. A few are caught each season. The writer had the opportunity to examine one caught in East Okoboji Lake in August, 1925.

Ameiurus natalis (Le Sueur). Yellow Bullhead; Yellow Cat

This bullhead prefers water of moderate depth with muddy bottom in or near the water plants. Its range extends into deeper waters than that of the other bullheads. It is common in both East and West Okoboji Lakes, and occurs in lesser numbers in Spirit Lake.

Ameiurus nebulosus (Le Sueur). Common Bullhead

The common bullhead shows a preference for the same conditions as *natalis* but is found more commonly in shallow water. It is toler-

ably common in all the major lakes, but was found especially common in the shallow weedy Robinson and Hottes Lakes. Here, in 1922, the local fishermen came for their market supply of bullheads.

Ameiurus melas (Rafinesque). Black Bullhead

Like the other bullheads, this one prefers muddy bottom ranging in depth somewhat between the other two, although seined from as shallow water as the common bullhead. It is the commonest of the bullheads in Spirit Lake and occurs rather commonly in the other major lakes.

Leptops olivaris (Rafinesque). Flathead Cat

The writer has not collected any of this species. Apparently it was introduced accidentally with shipments of the channel cat, *I. punctatus*. As noted in the discussion of the latter, individuals of the flatheads were also taken in the gill nets in the winter of 1917-18. Mr. Hopkins reported one caught in East Okoboji Lake in the winter of 1925-26.

Esox lucius Linnæus. Common Pike; Northern Pickerel

This fish occurs commonly in the lakes, preferring the weedy portions which constitute its typical habitat. It is a swift predaceous fish which lies in wait for its prey, mainly fish, capturing it with a quick dash. The subcylindrical shape of the body fits it for moving in between the stems of the water plants without hindrance. This shape may be of further aid to the fish because of its resemblance to a submerged stick, which would be increased by its habit of remaining nearly motionless in the water. Thus its unsuspecting victim might approach within capturing distance.

Fundulus diaphanus menona (Jordan & Copeland). Menona Top-minnow

The top-minnow is found most commonly in the shallow water with a sandy bottom, either in the weeds or between them and the shore. It occurs commonly along the sand-bar in Miller's Bay, West Okoboji Lake during August, and less commonly earlier in the season. It was seined also in East Bay, Spirit Lake, and in Hottes Lake.

Meek recorded *F. zebrinus* from East Okoboji Lake.¹³ None of the specimens taken by the writer could be referred to that species.

¹³ Meek, S. E. Notes on the Fishes of Western Iowa and Eastern Nebraska, p. 137.

Zebrinus has sixty scales in the lateral series and twenty-one transversely. There are fourteen or fifteen rays in the dorsal fin, and thirteen or fourteen in the anal.¹⁴ The specimens collected by the writer had from forty-two to fifty scales in the lateral and twelve to fourteen in the transverse series. The dorsal had twelve to thirteen rays and the anal ten to eleven. If Meek was correct in his identification, apparently *menona* has supplanted *zebrinus* completely or nearly so. The occurrence of the latter seems doubtful enough to warrant its omission.

Eucalia inconstans (Kirtland). Brook Stickleback

This stickleback was seined commonly in shallow water over a mud bottom in Swan Lake, Dickinson County, in August, 1924. This lake is in the drainage system of the Des Moines River. However, the species is included here because Mr. Hopkins had taken it in Reed Creek before the sloughs, once characteristic of it, were drained.

Percopsis guttatus Agassiz. Trout Perch

One specimen of this species has been taken in the lakes by the writer. This was seined in East Bay, Spirit Lake, July 21, 1921, in water between one and two meters deep, over a sandy bottom and near water weeds. Twelve other individuals were taken in the Little Sioux River, July 28, 1922. Meek in his list includes the statement of Evermann regarding this fish. On November 2, 1892, the latter found four specimens in the minnow box of a hotel. He states further that Mr. H. E. Owen, then proprietor of the Lake Park House of Spirit Lake, reported the species as "abundant in the lakes."¹⁵ While this statement may have applied at that time, it certainly does not now for the trout perch is evidently uncommon at present.

Pomoxis annularis Rafinesque. White Crappie; Crappie

The crappie is common in all the major lakes. It shows a preference for water four to six meters deep with a muddy bottom, in or near water weeds. It comes into shallower water for feeding in the evening.

¹⁴ Jordan, D. S. and Everman, B. W. Fishes of North-Middle America, Vol. I, p. 646.

¹⁵ Meek, S. E. Notes on the Fishes of Western Iowa and Eastern Nebraska, p. 137.

Pomoxis sparoides (Lacepede). Black Crappie; Calico Bass

This species has not appeared as frequently as the preceding one in seining. Its habitat is similar to that of the white crappie with which it is frequently confused. Besides its darker markings, this species has the anal fin reticulated with dark greenish markings, while the anal fin of *annularis* is nearly plain. *Sparoides* has seven or eight spines in the dorsal fin, *annularis* six.

Ambloplites rupestris (Rafinesque). Rock Bass

Only three individuals of this species have been taken, all from Miller's Bay, West Okoboji Lake. It is said by Mr. Shear, to occur in limited numbers in all the major lakes. It prefers moderate depths with rocky bottom.

Apomotis cyanellus (Rafinesque). Green Sunfish

This sunfish is generally found in or near water weeds, ranging from near the shore line to a depth of three to four meters. It shows a preference for a sandy silt bottom. It is a common fish in the weedy bays of West Okoboji and occurs less commonly in East Okoboji and Spirit Lakes.

Lepomis megalotis (Rafinesque). Long-eared Sunfish

This fish shows a preference for shallow weedy waters, with a bottom of mud or sandy silt. In 1922, it was taken in considerable numbers in Robinson Lake, fifty-five at one drag of the seine. Several were also seined in North Hottes and two in East Okoboji. It was not recorded elsewhere.

Lepomis humilis (Girard). Red-spotted Sunfish

The red-spotted sunfish has been recorded only from the Little Sioux River. In 1924, seven adults were seined in the west branch of the river, in water from one to one half meters deep. In August of the next year, six young of that season were taken from a pool in the otherwise dry bed of the river.

Lepomis pallidus (Mitchill). Bluegill

With the exception of the perch, the bluegill is the most abundant fish in the three major lakes. It has not been recorded from any of the smaller ones. It is found under a variety of conditions of depth and bottom. It is frequently taken in the shallow water around docks, but its more characteristic habitat is in or near the growths of water weeds.

Eupomotis gibbosus (Linnaeus). Common Sunfish; Pumpkin-seed

This is a characteristic fish of the weedy portions of the major lakes, in water of shallow to moderate depth, and in the shallow weedy lakes, Robinson and Hottes. Like the bluegill, it is found over different types of bottom ranging from mud to sand.

Micropterus dolomieu Lacepede. Small-mouthed Bass

Meek records this species as follows, "Among the waters covered by this report, the small-mouthed bass was found only in Spirit Lake."¹⁶ It has not been recorded by the writer, but is reported by Mr. Shear as occurring rarely, through accidental introduction with the large-mouthed bass. Every few years, according to his statement, one of this species is caught here.

Micropterus salmoides (Lacepede). Large-mouthed Bass

This is one of the best and most important game fishes of this region. It is tolerably common in the three major lakes. It prefers the weedy portions of the lake, but is not limited to them, and may be found over different types of bottom.

Stizostedion vitreum (Mitchill). Wall-eyed Pike; Pike

This is the most important game fish of the lakes, and occurs in considerable numbers in the three major lakes. The State Fish Hatchery at Orleans is maintained wholly for the propagation of this fish. In 1922, 9,000,000 fry were liberated in West Okoboji, 5,000,000 in Spirit Lake, and 3,000,000 in East Okoboji.¹⁷ The spawning season begins soon after the ice is out of the lakes, the fishes coming into shallow water near the shore for this purpose. During the summer, they migrate to deeper water where the bottom is rocky.

Stizostedion canadense griseum (De Kay). Sauger

The sauger has not been taken by the writer in this region, and but one specimen, a mounted one owned by its captor, Mr. Harry Tennant, of Arnold's Park, has been examined. It is mentioned by Meek as occurring in Spirit Lake,¹⁸ and by Carfield in his letter to the State Game Warden. It is reported by Mr. Shear as tolerably

¹⁶ Meek, S. E. Notes on the Fishes of Western Iowa and Eastern Nebraska, p. 138.

¹⁷ Figures supplied by Dr. John H. Malony, State Fish and Game Dept.

¹⁸ Meek, S. E. Notes on the Fishes of Western Iowa and Eastern Nebraska, p. 138.

common in the lakes. Very likely it is not commonly distinguished from the other species.

Perca flavescens (Mitchill). Yellow Perch; Perch

This is the commonest and most widely distributed of all the fishes in the lakes. It is found under a variety of conditions of bottom, from mud as in North Hottes to sandy as in Spirit Lake, and from shallow water one and one half meters to nearly twenty-seven meters (eighty-seven feet) in Emerson Bay of West Okoboji. It may also be found in or near the growth of water weeds or away from them. It attains its largest size in Spirit Lake. A young individual, 40 mm. long, was taken in Thomas Creek, July 20, 1922.

Percina caprodes (Rafinesque). Sand Darter; Log Perch

This species is found on sandy or gravelly bottom in shallow water. It is abundant in Spirit Lake, where it was seined most commonly in water from one to one and one half meters deep. It was not taken in East Lake, although it probably occurs there. Only one specimen was taken in the West Lake. This was seined along the Sand-bar by Messrs. D. T. Jones and G. E. Potter, August 12, 1924.

Boleosoma nigrum (Rafinesque). Johnny Darter

Meek records this species from both East Okoboji and Spirit Lakes. "A specimen was found in a minnow basket at Spirit Lake where it seems to be used as live bait to some extent."¹⁹ It was not taken by the writer in the lakes but was seined in the Little Sioux River in the summers of 1924 and 1925.

Etheostoma iowae Jordan and Meek. Iowa Darter

Meek collected this species in Spirit Lake, but gives no data concerning it.²⁰ The writer has not collected it personally but has in his possession six specimens collected by Mr. Hopkins in Spirit Lake, May 12, 1926. He states that he has seen this species in late spring or early summer in East Okoboji Lake, in shallow water over sand between the weeds and the shore.

Roccus chrysops (Rafinesque). Silver Bass; White Bass

This is a common species in both East and West Lakes, less so in Spirit Lake. On June 26, 1922, 200 were taken in the seine in East

¹⁹ Meek, S. E. Notes on the Fishes of Western Iowa and Eastern Nebraska, p. 138.

²⁰ Loc. cit.

TABLE I
Summary of Distribution

Species	West Okoboji	East Okoboji	Spirit	Hottes	Reed Creek	Thomas Creek	Little Sioux River
<i>P. spathula</i>	x?	x?					
<i>L. osseus</i>	x	x	x				
<i>L. platystomus</i>	x	x	x				
<i>H. alsoides</i>		x					
<i>C. namaycush</i>	x?	?	x?				
<i>I. cyprinella</i>	x	x	x	x			
<i>I. bubalus</i>	x	x	x				
<i>Carpiodes carpio</i>							x
<i>C. commersonii</i>	x	x	x				x
<i>M. aureolum</i>	x	x					x
<i>Cyprinus carpio</i>	x	x	x				x
<i>H. nuchalis</i>							x
<i>P. notatus</i>		x	x	x			x
<i>S. atromaculatus</i>					x	x	x
<i>A. crysoleucas</i>	x	x	x	x			
<i>C. vigilax</i>	x	x	x				
<i>N. cayuga</i>	x			x			
<i>N. heterodon</i>	x	x					
<i>N. blennius</i>	x				x	x	x
<i>N. hudsonius</i>	x	x	x				
<i>N. lutrensis</i>	x	x					x
<i>N. jejunos</i>	x						
<i>R. atronasmus</i>					x	x	
<i>H. storerianus</i>		x					x
<i>I. punctatus</i>	x	x	?				x
<i>A. natalis</i>	x	x	x				
<i>A. nebulosus</i>	x	x	x	x			
<i>A. melas</i>	x	x	x				x
<i>L. olivaris</i>	x	x					
<i>E. lucius</i>	x	x	x	x			
<i>F. diaphanus</i>	x	x	x	x			
<i>E. inconstans</i>					x?		
<i>P. guttatus</i>		x	x				
<i>P. annularis</i>	x	x	x				
<i>P. sparoides</i>	x	x	x				
<i>A. rupestris</i>	x	x	x				
<i>A. cyanellus</i>	x	x	x				
<i>L. megalotis</i>		x		x			
<i>L. humilis</i>							x
<i>L. pallidus</i>	x	x	x				
<i>E. gibbosus</i>	x	x	x	x			
<i>M. dolomieu</i>			x				
<i>M. salmoides</i>	x	x	x				
<i>S. vitreum</i>	x	x	x				
<i>S. canadense</i>		x	x				
<i>P. flavescens</i>	x	x	x	x	x	?	
<i>P. caprodes</i>	x	x	x				
<i>B. nigrum</i>		x	x				x
<i>E. iowæ</i>		x	x				
<i>R. chrysops</i>	x	x	x				
<i>A. grunniens</i>	x	x	x				
Totals	36	40	33	10	5	3	14

TABLE II
Summary of Habitat of Lake Fishes

Species	Mud	Sand	Rock	Open	Weedy
<i>P. spathula</i>	x				
<i>L. osseus</i>	x	x			x
<i>L. platystomus</i>	x	x			x
<i>C. namaycush</i>				x	
<i>I. cyprinella</i>	x				x
<i>C. commersonii</i>			x	x	
<i>Cyprinus carpio</i>	x				x
<i>P. notatus</i>	x				x
<i>A. crysoleucas</i>	x				x
<i>C. vigilax</i>	x	x		x	x
<i>N. cayuga</i>	x	x		x	x
<i>N. heterodon</i>	x	x		x	x
<i>N. blennius</i>		x		x	
<i>N. hudsonius</i>		x		x	x
<i>N. lutrensis</i>		x		x	
<i>I. punctatus</i>	x			x	
<i>A. natalis</i>	x			x	x
<i>A. nebulosus</i>	x			x	x
<i>A. melas</i>	x			x	x
<i>L. olivaris</i>	x			x	
<i>E. lucius</i>	x	x		x	x
<i>F. diaphanus</i>		x		x	x
<i>E. inconstans</i>	x				x
<i>P. guttatus</i>		x		x	
<i>P. annularis</i>	x		x	x	x
<i>P. sparoides</i>	x		x	x	x
<i>A. rupestris</i>		x	x	x	x
<i>A. cyanellus</i>		x		x	x
<i>L. megalotis</i>	x				x
<i>L. pallidus</i>	x	x		x	x
<i>E. gibbosus</i>	x	x			x
<i>M. salmoides</i>	x	x		x	x
<i>S. vitreum</i>			x	x	
<i>P. flavescens</i>	x	x	x	x	x
<i>P. caprodes</i>		x		x	
<i>B. nigrum</i>		x		x	
<i>E. iowæ</i>		x		x	
<i>R. chrysops</i>	x		x	x	x
<i>A. grunniens</i>	x		x	x	
Totals	26	20	8	29	26

Okoboji near the outlet of Spirit Lake in water from one to two meters deep over sandy bottom. Later in the season they prefer somewhat deeper water, under different conditions of bottom. On July 20, 1922, they were caught in abundance in water three to four meters deep, over a muddy bottom. They were also being caught near a rocky point at the outlet of East Okoboji into the Upper Gar Lake, where the water was six or seven meters deep.

Aplodinotus grunniens Rafinesque. Sheepshead ; Fresh-water Drum

The sheepshead is common in East and West Okoboji Lakes, but is rather rare in Spirit Lake. It was not recorded elsewhere. It is found more commonly in moderate depths over both muddy and rocky bottom.

The observations regarding the distribution and habitat of the fishes of this region are summarized in Tables I and II. The occurrence of the species is indicated by the letter "x". Species marked "x?" have occurred here but are doubtfully present now. Those marked "?" may occur but have not been found or reported and are not included in the totals. Table II includes only those lake fishes for which definite data were obtained. These observations apply to the summer season only.

THE FISHES OF REED AND THOMAS CREEKS

On the east side of East Okoboji Lake are two small creeks which flow into the lake within a half mile of each other. These will be designated as Thomas and Reed Creeks respectively, the names given to them in the past from owners of the adjoining land. These creeks resemble each other in their physical features, so that a common description, in the main, will serve for the two. Both are small creeks with bottoms mainly of silt with some intermixture of sand. They are narrow and shallow with occasional deeper pools and with slightly developed riffles in places where the flow, otherwise rather sluggish, becomes moderately fast. Near the lake, the creeks flow through a wooded tract in which the dominant type of tree is the bur oak, *Quercus macrocarpa*. Of the two, Thomas Creek is the larger, with larger, deeper, and more numerous pools, and with a more rapid current. Just before entering the woods, this creek is fed by four springs.

This latter creek was first visited by the writer in the summer of 1921. During the seasons of 1922 and 1924, both creeks were visited and collections made, temperature taken, and samples of the water taken. In 1922, the samples were tested by the Winkler method for their oxygen content by Mr. Wesley Damerow. In 1924, others were tested by Miss Josephine Bockwoldt for the hydrogen ion concentration. These tests indicate a high hydrogen ion concentration. It seems probable that this may be accounted for by the boggy ground through which, for a part of their course, the creeks flow. The results of these tests as well as the temperature reading and the weather conditions are given in Table III.

TABLE III
A. Reed Creek

Date	Time	Weather	Wind	Air temp.	Water temp.	O cont.	H. ion conc.
7/20/22	1:15 P.M.	Fair	Light, S.	*	*	6.70	
8/2/22	9:30 A.M.	Clear	Calm	29°C.	17°C.		
8/12/22	11:10 A.M.	Clear	Light, S.	29°C.	21°C.	9.38*	
						8.98	
7/28/24	11:15 A.M.	Clear	Light, S. E.	31°C.	18°C.		5.32
8/4/24	9:45 A.M.	Clear	Light, S.	29°C.	16°C.		4.78
8/12/24	2:00 P.M.	Clear	Light, N. E.	26°C.	19°C.		
8/14/24	3:20 P.M.	Hazy	Strong, S.	28.5°C.	20.5°C.		

B. Thomas Creek

Date	Time	Weather	Wind	Air temp.	Water temp.	O cont.	H. ion conc.
7/20/22	2:30 P.M.	Fair	Light, S.	*	**	7.63	
8/4/24	10:00 A.M.	Clear	Light, S.	28°C.	22°C.		4.76
8/12/24	2:30 P.M.	Clear	Light, N. E.	25°C.	23°C.		
8/14/24	3:55 P.M.	Hazy	Strong, S.	27°C.	22°C.		

* Thermometer broken

** Two samples taken

The fish found in the two creeks were nearly identical. Four species were recorded from both and a fifth one from Reed Creek. In both the main species were the creek chub, *Semotilus atromaculatus*, the black-nosed dace, *Rhinichthys atronasus*, and the straw-colored minnow, *Notropis blennius*. An immature perch, *Perca flavescens*, 40 mm. long, was taken in Thomas Creek about three fourths of a mile from the mouth. Mr. Hopkins has taken adult perch in Reed Creek near the mouth, in the spring when the water was high, and it probably comes into the other creek under similar conditions. Mr. Hopkins also has taken the brook stickleback, *Eucalia inconstans*, in past years from Reed Creek. The writer has no evidence whether or not it still occurs here. The distribution of the fishes in the two creeks was similar. The great majority of the creek chub and the black-nosed dace was found in the deeper pools where they could find shelter under the overhanging shelves formed by the grasses and other herbaceous plants, or by the roots of adjoining trees. The straw-colored minnows showed a preference for the swifter waters of the creek, and were frequently observed in or near the riffles, although a few were taken in the pools with the other two species. Of the three, the creek chub was the most numerous, the black-nosed dace next in abundance, with the straw-colored minnow the least common.

The food of seventeen fishes from Reed Creek was studied. Of these, thirteen were creek chubs, three were straw-colored minnows, and the remaining one a black-nosed dace. The results are summarized in Table IV.

TABLE IV
Food of Seventeen Fishes from Reed Creek

Species	Total length in mm.				Water		Clado-	Cope-	Cray-	Insects	Hydra-
	No.	Mn.	Mx.	Av.	Algæ	Weed	cera	podæ	fish	Larva	Adult carina
<i>S. atromaculatus</i>	13	25	91	46.1	0.66	1.3			5	35.4	57.5 *
<i>E. atronasus</i>	1			73.0						12.0	88.0
<i>N. blennius</i>	3**	24	45	36.6	Traces		1.5	0.5		95.0	3.0

* One individual was found in the thirteen fishes examined

** One with stomach and intestines nearly empty; remaining contents unidentifiable; percentages based on two specimens

The food of the creek chub, as indicated in the table, consisted largely of insects, 92.8% in all. Of the thirteen studied, three had eaten only adult insects, and in two others, these formed 96% and 98% respectively. The insects eaten were almost wholly either aquatic coleoptera, mainly *Gyrinidæ*, or water-boatmen, *Corixa* sp. One individual, not of the five mentioned, had eaten a grasshopper. Insect larvæ constituted all the food in one specimen, and 90% and 97% respectively in two others. Fully 90% of these were chironomid larvæ, the remainder consisting of other dipterous larvæ and the nymphs of water-boatmen. Another individual had eaten crayfish and also some filamentous algæ, *Vaucheria*.

Forbes and Richardson speak of this fish as having "an unusually varied diet for a minnow, including considerable quantities of vegetable food on the one hand and small fish on the other. A fourth of the food of twenty-two specimens consisted of algæ and of miscellaneous vegetable debris. Four of the specimens had eaten little else than filamentous algæ, and three had captured small fishes. Grasshoppers, caterpillars, ants, chrysomelid and scarabæid beetles, and various other terrestrial insects together with *Corisa*, dipterous larvæ, and other aquatic forms, were the insects represented, and three of the twenty-two specimens had eaten only crayfishes."²¹ Everman and Clark state "the principal food of the chub consists of insect larvæ, aquatic insects, worms, and small crustaceans."²²

The numbers of the other two species are in themselves too small

²¹ Forbes, S. A. and Richardson, R. E. Fishes of Illinois, p. 123.

²² Evermann, B. W. and Clark, H. W. Lake Maxinkuckee, a Physical and Biological Survey, vol. 1, p. 346.

for definite conclusions. In the case of one of these, *Notropis blennius*, other data are available, which tend to confirm the result obtained by the writer. Forbes and Richardson state, "from the little that is known of its feeding habits, its food is no more peculiar than its general appearance, consisting of a mixture of aquatic insects, and chance vegetation."²³ In an earlier paper Forbes gives the results of a study of five of these minnows. Seventy-five per cent of the food was animal matter, the remaining plant, mainly grass seeds.²⁴ Of the former, insect larvæ constituted 58% and copepods, almost wholly *Cyclops*, 10%.

These three fishes are typical pioneer fishes characteristic of young streams such as the two creeks studied. Shelford, some years ago, pointed out that the creek chub, *Semotilus atromaculatus*, is the species "most commonly found in the smallest streams and nearest the headwaters of the larger streams."²⁵ In most cases the red-bellied dace, *Chrosomus erythrogaster*, which is not found here, was the next one to be found as one went downstream from the source, but in some he found the black-nosed dace, *Rhinichthys atronasus*, to be the second species. In one stream, too, the straw-colored minnow, *Notropis blennius*, was one of six species to be found in the first mile from the source. In Reed and Thomas Creeks, the range of these three species coincided, although the relative numbers of the creek chub were somewhat greater in the uppermost pools. During the two seasons the conditions under which they lived were nearly similar. The temperature of the water was low especially in the pools of Reed Creek. The oxygen content of the water was high with apparently a high hydrogen ion concentration also. Stretches of gravel or sand, which occur occasionally, furnish favorable spawning beds, and during the summer there is an abundant supply of insect food which appears to be the chief food item at this season.

THE OKOBOJI LAKES

The Okoboji Lakes, products of the Wisconsin ice sheet, include three major lakes, Spirit, East and West Okoboji, and several minor ones. The West and East Lakes are connected by a narrow channel between the towns of Arnold's Park and Okoboji. There is a creek

²³ Forbes, S. A. and Richardson, R. E. Fishes of Illinois, p. 138.

²⁴ Forbes, S. A. The Food of smaller Fresh-water Fishes. Bull. III, III. State Lab. Nat. Hist., Vol. I, p. 65-94, 1883.

²⁵ Shelford, V. E. Ecological Succession. I, Stream Fishes. Biol. Bull., Vol. 21, p. 9-25, 1911.

between Spirit Lake and East Lake through which a small stream of water flows, when the level of the former lake is high enough. During the summer seasons of 1924 and 1925, there was little or no water in this runway. These lakes drain through the Gar Lake with which East Lake is connected, into the Little Sioux River. The amount of water which goes into this river is said to be slight in comparison with the amount lost from the lakes through evaporation. Welch Lake to the north of, and Center Lake to the east of West Okoboji Lake, have poorly developed streams through which a small amount of water flows into the latter. To the west and north-west of Spirit Lake are five of the minor lakes, Little Spirit, Hottes, Robinson,²⁶ Marble, and Sunken. These drain into Spirit Lake, the last four through Hottes Lake. During the seasons referred to before, the level of these four lakes was lowered so that they are entirely cut off from each other, and Hottes Lake itself from Spirit Lake. The total drainage area of the lakes is not great, 84,500 acres²⁷ or 132 square miles. In Table V the size and depths of the lakes are given. With the exception of West Okoboji, the areas were taken from the Iowa Lake Bed Report, 1917 and the other figures are based on studies made of the maps of the State Highway Commission.

TABLE V
Size and Depth of the Lakes

Name of Lake	Area in acres	Length of shoreline in miles	Volume in cubic meters	Maximum depth in meters	Mean depth in meters
Spirit	5660	18.3	225,548,000	7.6	5.5
West Okoboji ²⁸	3788	18.2	188,340,000	40.2	12.3
East Okoboji	1875	16.7	22,687,000	7.9	3.0
Center	264	2.6	3,567,000	4.5	3.2
Welch	57	1.4	344,000	1.9	1.5
Little Spirit	724*	10.4	5,132,000	3.7	2.1
Hottes	312	7.0	1,758,000	2.4	1.4
Marble	175	2.7	1,058,000	2.1	1.5

* 214 acres only in Iowa, the remainder in Minnesota.

Some years ago Shelford traced the ecological succession in several sand-bottomed ponds located in Indiana near the south end of

²⁶ The west portion of Hottes Lake as shown on maps 23-24, State Highway Commission, 1915.

²⁷ Iowa Lake Bed Survey Report, 1917, p. 54.

²⁸ Birge, E. A. and Juday, Chancey. A Limnological Reconnaissance of West Okoboji. Stud. in Nat. Hist., Univ. of Ia., Vol. IX, No. 1, p. 5, 1920.

Lake Michigan.²⁹ In the earliest stage the bottom was free of plant growth. This was followed by a stage in which the bottom was overgrown with *Chara*, frequently associated with a growth of bulrushes near the edge of the pond. This, as Shelford states, "prepares a way for the vegetation which reaches to and above the surface. This, in turn, fills the pond still further and the strictly marsh vegetation takes possession. The history of the true pond is then at an end and the story of the marsh begins."³⁰

Some of these ecological stages may be found in the lakes of the Okoboji region. The early bare-bottom stage is nearly realized in the case of Welch Lake. The bottom is mainly of silt with a slight intermixture of sand along the shore. On the west shore and to a lesser extent on the east side the bottom is rocky. The slope is gradual, and the greatest depth is not quite two meters. Filamentous algæ were noted on the rocks and other objects in the water but no *Chara* was found, and the aquatic seed plants were scarcely represented. Phytoplankton in which *Microcystis* predominated was very abundant, giving a greenish color to the water. The fish fauna is very limited. The bullhead minnow, *Cliola vigilax*, was seined by the writer in great numbers, and several young black bullheads, *Ameiurus melas*, were also taken. Mr. Shear, who for twenty years has seined this lake for minnows, states that with the exception of an occasional pike, *Esox lucius*, he has never taken other than these two species.

Another ecological stage much in advance of Welch Lake is represented by Spirit Lake. This lake, the largest in the state, is shallow in comparison with its size, reaching a depth of only 7.6 meters. With the exception of East Bay the outline is very regular. The shores are comparatively low so that it is exposed to winds from all directions. The bottom of the shallower waters is chiefly sandy although gravel, both coarse and fine, and clay occur. The slope of the bottom is very gradual. There are several rock reefs in the lake, mainly in deeper water although a few of them reach the shore.

While the amount of vegetation other than the phytoplankton and attached filamentous algæ is relatively moderate, well developed growths of water weeds and of rushes are found in different portions

²⁹ Shelford, V. E. Ecological Succession. II, Pond Fishes. Biol. Bull., 21, p. 127-151, 1911.

³⁰ Shelford, V. E. Animal Communities in Temperate America, p. 151, 1913.

of the lake. The phytoplankton in the summer time becomes so abundant as to form a green scum on the surface of the calm water. Shimek accounts for the moderate growth of the higher plants by the lack of sheltered bays, "coupled with the prevailing sandy or gravelly shores and bottom, and the greater exposure of the surface to storms."³¹

While earlier ecological stages may be found, the lake as a whole has reached the stage of early maturity. The conditions are evidently favorable for fish life, for thirty-three species representing twelve families have been recorded from this lake. It is extremely doubtful, however, that one of these, the Great Lake Trout, *Cristivomer namaycush*, is found here at the present time.

West Okoboji Lake presents conditions markedly different from the two lakes already discussed, and in the matter of depth differs from all of the lakes of this region. Its mean depth, 12.3 meters, is greater than the maximum of any other of these lakes, and it reaches a maximum depth of 40.2 meters. West Okoboji is nearly six miles long, and while it is three miles across in its widest portion, its average width is approximately a mile. It is not so exposed as Spirit Lake, its bank for the most part high, abrupt, and wooded, although in several places the land slopes down to the water's edge. The outline of this lake is irregular. Three well developed bays cut off to a greater or less extent by points of land and outstretching reefs are found on the southeast and west shores. Smaller bays and coves also occur on either side of the lake. "The main slope of the bottom of the lake is fairly uniform to the depth of eighty feet, but below that depth the slopes are decidedly steeper."³²

West Okoboji has attained the stage of maturity, although in different localities other stages from the bare-bottom to that of the marsh may be found. More favorable conditions for aquatic vegetation are afforded in this lake than in Spirit Lake. The bottom is not so uniformly sandy here, and there is better protection from wave action, especially in the three bays referred to. Wylie concluded from a survey made of the lake that about 1100 acres, about 30% of the lake, was occupied by the larger plants. In most places, he states, these are submerged and do not come to the surface.³³

³¹ Shimek, Bohumil. The Plant Geography of the Lake Okoboji Region. Bull. from Lab. Nat. Hist., Univ. Ia., Vol. VII, No, p. 5, 1915.

³² Birge, E. A. and Juday, Chancey. A Limnological Reconnaissance of West Okoboji. p. 5.

³³ Wylie, R. B. The Major Vegetation of Lake Okoboji. Proc. Ia. Acad. Sci., Vol. 27, p. 91-97, 1920.

The growth of phytoplankton becomes conspicuous from midsummer on, but not so marked, however, as that found in Spirit Lake.

A slightly larger number of fishes, thirty-six, has been recorded from this lake. This number includes again the Great Lake trout which has been planted in the lake with doubtful success. The great majority of fishes, both of species and individuals, are found in the bays in the vicinity of the water weeds.

East Okoboji is a long narrow lake, nearly seven miles in length, and averaging about one half a mile in width. It is irregular in outline and generally has high banks, many of them wooded. The lake is shallow with a maximum depth of 7.9 meters, and an average of 3.0 meters. This lake with its abundant growth of aquatic vegetation represents a stage of maturity in advance of the West Lake. Forty species of fish have been recorded from this lake.

The most advanced ecological stage which is represented here is found in the small shallow lakes, Marble, Hottes, and Robinson. The last named with which the author is most familiar will be used to illustrate this stage. When first visited, in 1922, Robinson Lake was about one and one half miles long and half a mile wide. It was very shallow, the greatest depth then less than two meters. The bottom, soft and mostly clay, with some sandy silt, was largely covered with a rich growth of water weeds. In some parts of the lake patches of rushes occurred. Six species of fish were taken in this lake. During the next three years the rainfall was so greatly reduced that the level of all the lakes was greatly lowered. Robinson and the adjoining shallow lakes were in danger of drying up completely and the fish life nearly, if not completely, exterminated. About twenty years ago under similar conditions, so the writer was informed, these lakes became dry. They are in the stage of old age, and are so shallow that they do not have sufficient volume of water to withstand a series of dry seasons.

GENERAL DISCUSSION

The results obtained from these studies indicate that a large number of species prefer a habitat in or near the growths of water weeds.³⁴ Of the forty-five species listed from the lakes here, twenty-six are found there all or part of the time, while twelve show a preference for open water. The writer has no data for the remaining seven species. Wylie, in his survey of the vegetation of Lake

³⁴ Potamogetons, *Myriophyllum*, and *Ceratophyllum* are the dominant types.

Okoboji, made the following observation: "During the entire month given to this survey, and during which time hundreds of people were observed fishing in various parts of Lake Okoboji, no fish were being caught except in or along the edge of these masses of major vegetation."³⁵ There are two evident advantages derived from a habitat among the aquatic plants. In the first place, it affords a wide range of food possibilities, and secondly, it provides excellent shelter. Predaceous species as the Pike, *Esox lucius*, concealed by vegetation, lie in wait for their prey. Other species as the carp, *Cyprinus carpio*, lay their eggs in such places, and the nests of the sunfishes may be found in shallow water near the shore among the water plants. While the differences in the numbers of species recorded from the three major lakes are not large enough to be significant, yet it is interesting to note that their order coincides with the relative amount of vegetation found. Thus Spirit Lake with a moderate amount of vegetation has thirty-three species of fishes, West Okoboji with a large amount, thirty-six species, and East Okoboji with relatively the greatest amount, has forty.

Robinson Lake with a proportionately greater growth of vegetation than East Okoboji, might be expected to have a greater number of species than the latter, but only six species were taken there.³⁶ The most conspicuous difference between the two is that of depth, Robinson having a maximum depth of 1.6 meters while that of East Okoboji was 7.9 meters. While the difference in depth may be a factor in accounting for the greater number of species in the one than in the other, it seems probable that other factors are more concerned. The oxygen content of the water is probably favorable, for two samples taken from different parts of the lake on August 12, 1922, gave 5.07 and 5.22 cc. per liter. Another sample taken July 28, 1924, and tested for the hydrogen ion concentration, gave a pH of 5.71. This degree of acidity is probably an important factor in limiting the number of species. Possibly the high temperature of the lake at times during the summer is another factor. On July 27, 1922, at 2:15 P. M., the surface temperature near the shore was thirty-one degrees, C., one degree cooler than the air, and on August 14, 1924, at 2:20 P. M., the same temperature was noted with an air temperature of twenty-seven degrees, C. Three of the species

³⁵ Wylie, R. B. The Major Vegetation of Lake Okoboji. Proc. Ia. Acad. Sci., Vol. 27, p. 97, 1920.

³⁶ These and the following statements apply to conditions in 1922.

found in this lake occurred in great numbers, namely, the black bullhead, *Ameiurus melas*, the long-eared sunfish, *Lepomis megalotis*, and the common sunfish, *Eupomotis gibbosus*. Two others, the perch, *Perca flavescens*, and the golden shiner, *Abramis crysoleucas*, were tolerably common, and the pike, *Esox lucius*, was found in lesser numbers. Evidently the conditions were favorable for these fishes, but were not the kind preferred by other species, for opportunity in the past has been given them to enter this lake at the time of high water when Robinson, Hottes, and Marble Lakes were connected with each other and with Spirit Lake.

Under certain conditions of weather the oxygen content of Spirit Lake apparently becomes so reduced as to make conditions for the fishes most unfavorable. Under ordinary conditions the oxygen supply is kept up in part by photosynthesis in the water plants and in part by wave action. Exposed as it is on all sides, the surface for the most part is kept in motion and the oxygen distributed. The lake is too shallow for stratification during the summer and from the meager data available, the temperature and oxygen content appear to vary but little from the surface to the bottom under ordinary conditions.

For three or four days ending August 6, 1922, calm weather prevailed with high temperature. On the 6th, Dr. J. H. Malony reported that the wall-eyed pike, *Stizostedion vitreum*, were dying in great numbers in Spirit Lake and the perch, *Perca flavescens*, and the shiner, *Notropis hudsonius*, had suffered but not to such a marked extent. Specimens of the first two species were examined but nothing abnormal was discovered. On the 7th, when the writer visited the lake, a strong northwest wind was blowing and the lake was too rough to venture out on it. Larger fishes than those examined on the preceding day were washed in together with great numbers of smaller ones. Among them, black bullheads, *Ameiurus melas*, eight or ten inches long were noted. The number of dead fishes washed in decreased during the day until in the afternoon it was apparent that no more fish were dying.

Dr. G. M. Smith, who visited the lake on the morning of the 7th, came to the conclusion that decomposition of algæ was responsible for the death of the fishes. Exposure to the sun during the calm days had killed the phytoplankton so extensively that its decay in the water had consumed much of the oxygen present. At the same time the high temperature of the water during this period would

also tend to diminish the oxygen. It seems probable that the oxygen was so reduced during the period of calm ending the 6th, as to suffocate the fish.

On the 8th, the writer accompanied Professor F. A. Stromsten and Mr. Wesley Damerow to this lake where temperatures at different depths were taken with an electric resistance thermometer and samples of water taken for determination of the oxygen content. The results are given in the following table.

TABLE VI
Temperature Readings and Oxygen Content, Spirit Lake

Depth	Midway between Templar's Park and Red Nose Point 9:30 A.M.		East of Templar's Park 2:30 P.M.	
	Temp.	O cc. per liter	Temp.	O cc. per liter
0 m.	21.88°C.	5.61	23.50°C.	7.92
1 m.	21.80°C.	5.84	22.00°C.	
2 m.	21.85°C.	5.47	21.55°C.	
3 m.	21.80°C.	5.28	21.39°C.	4.99
4 m.	21.75°C.	5.62	21.30°C.	
5 m.	21.60°C.	5.85	21.20°C.	
6 m.			21.00°C.	3.67

It will be noted that the temperature varied but little from the surface to the bottom, and that the oxygen supply was evidently ample. It seems probable that the oxygen supply, which had been diminished in the ways mentioned, was restored to normal by the gale on the 7th. This stirred up the lake so that the oxygen was mixed with the water, and viable conditions once more established for the fishes. A similar occurrence under like conditions took place in early July 1921, but with less fatality to the fishes.

The number of species found in the Little Sioux River was much less than the number in the major lakes. Only twelve species were found in the river as compared with forty-five in the three lakes together. This is quite in accord with the observations of Pearse who states, "rivers, at least in summer, contain fewer fishes per unit of area than lakes. For fishes a river is a highway and a refuge. It gives access to the stores of food in swamps and lakes, and in winter furnishes an environment which is fairly stable. However, a river is not capable of producing much fish food within itself. The food resources available to lake fishes in the bottom mud cannot occur in quantity in rivers because the bottom is continually changing."³⁷

³⁷ Pearse, A. S. The Distribution and Food of the Fishes of Three Wisconsin Lakes in Summer. Univ. Wis. Stud. in Sci., No. 3, p. 53, Madison, 1921.

It will be noted, however, that Robinson Lake had but half the number of species found in the Little Sioux River, again indicating that the conditions in that lake were not favorable for a large number of species.

SUMMARY

Fifty-one species, possibly fifty-two, distributed among seven orders, fifteen families, and thirty-seven genera were recorded from the Lake Okoboji region. Of these, forty-five species were listed from the lakes, fourteen from the Little Sioux River, and five from Reed and Thomas Creeks. Two species, the small-mouth buffalo, *Ictiobus bubalus*, and the small-mouthed bass, *Micropterus dolomieu*, which were recorded by Meek, have not been taken by the writer. In the case of two other species, the spoonbill, *Polyodon spathula*, and the Great Lake trout, *Cristivomer namaycush*, the writer has no conclusive evidence to indicate whether or not they still occur in the lakes.

Observations were made regarding the summer habitat of thirty-eight species. Twelve were found to have a preference for muddy bottom, nine for sandy, and two for rocky. Nine species were found on both muddy and sandy bottoms, four on both muddy and rocky, one on both sandy and rocky, and another one was found on all three. Twenty-six species were found among aquatic vegetation, nine practically all the time and the remaining seventeen part of the time. Twelve showed a decided preference for open water. The preference for vegetation is presumably due to the abundance and variety of the food supply found there and to the shelter afforded by it.

During the summer season Reed and Thomas Creeks are narrow and shallow with occasional deeper pools and slightly developed riffles. Five species were listed from these creeks. Three of these, named in the order of the numbers found, the creek chub, *Semotilus atromaculatus*, the black-nosed dace, *Rhinichthys atronasus*, and the straw-colored minnow, *Notropis blennioides*, constituted the main fish life of both creeks. An immature perch, *Perca flavescens*, was taken in Thomas Creek. Adults of this species occur in the spring during high water in Reed Creek and very likely would be found in Thomas Creek under similar conditions. The brook stickleback, *Eucalia inconstans*, has been taken in years past in Reed Creek. Whether or not it occurs there now is uncertain. The brook chub

and the black-nosed dace were found mainly in the deeper pools with overhanging shelves of vegetation while the straw-colored minnow showed a preference for the swifter waters of the creeks. During the two seasons when the studies were made the conditions under which these three species lived were very similar. The temperature of the water was low, especially in the pools of Reed Creek. The water was well oxygenated and a high hydrogen ion concentration was indicated. The food, as judged by the stomach contents of seventeen of these fishes, consists mainly of insects during the summer.

Several ecological stages are represented by the different lakes of the Okoboji region. The earliest one, approximating the bare-bottom condition, is represented by Welch Lake. Three species of fishes were listed from this lake. Successive stages of maturity with increasing amounts of vegetation are found in Spirit, West Okoboji, and East Okoboji Lakes. The number of species of fishes recorded, while not markedly different, increased slightly with the greater amount of vegetation, thirty-three, thirty-six, and forty species respectively in the three lakes. The most advanced stage is found in the shallow lakes, Hottes, Robinson, and Marble. Robinson Lake, taken as a typical example, had but six species although the aquatic vegetation was relatively greater than that of East Okoboji. The acidity of the lake as indicated by a pH of 5.71 has probably been a factor in limiting the number of species here. The high temperature of the water at times during the summer, at least 31° C., associated with the extreme shallowness of the lake may be another factor.

Spirit Lake at times presents unfavorable conditions for fish life. A period of clear calm days with high temperature appears to kill the minute plants of phytoplankton. By the decay of these the oxygen supply of the lake is apparently reduced to such an extent that great numbers of fish are killed. The amount of oxygen supplied to the water through photosynthesis is not so great in this lake because of the rather moderate amount of vegetation. However, the lake is so exposed that under ordinary conditions there is a sufficient supply of oxygen through wave action.

The number of species of fishes found in the Little Sioux River was much less than that of the three major lakes. From Robinson Lake, however, less than half as many species were recorded as from the river.

BIBLIOGRAPHY

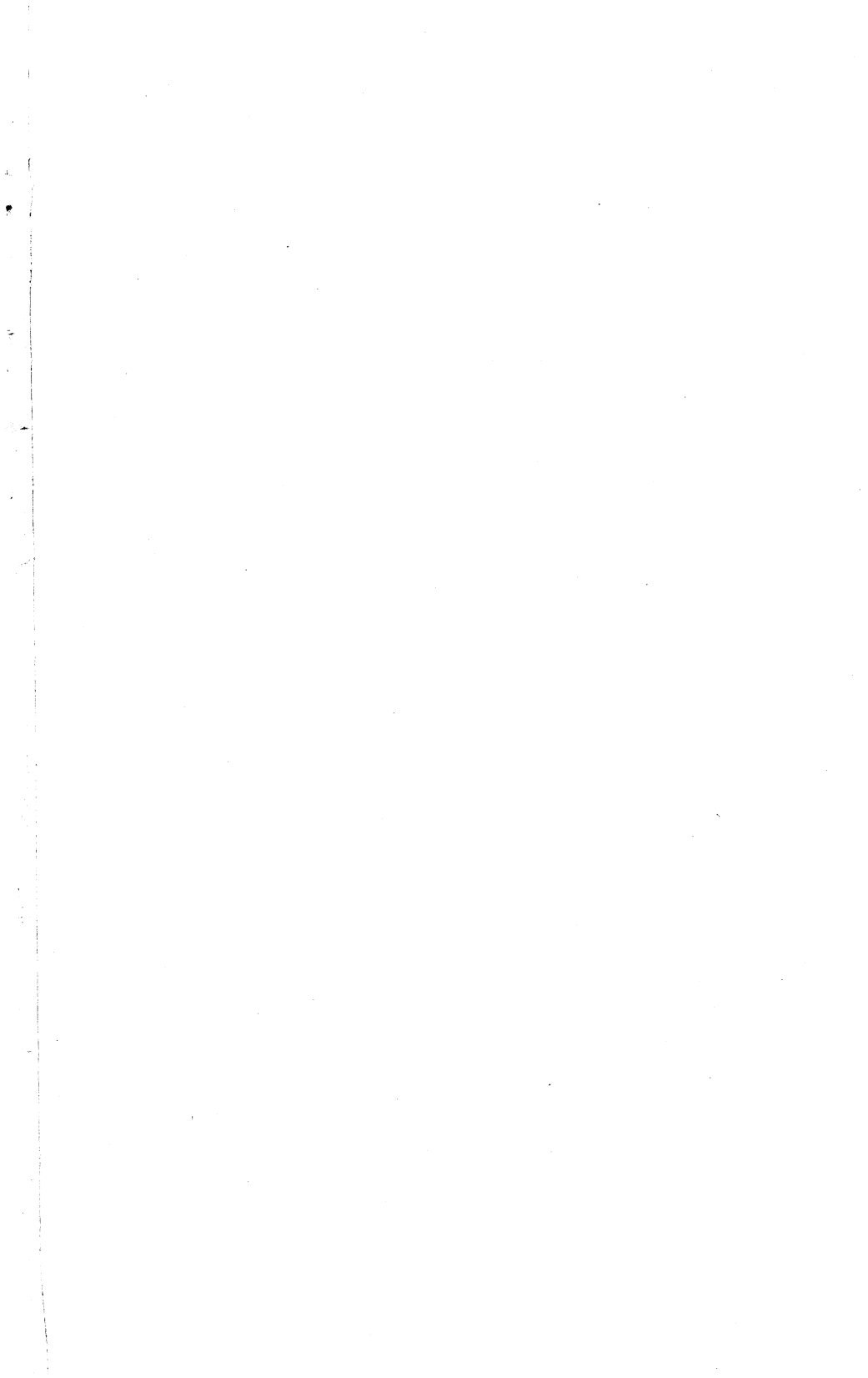
- Birge, E. A. and Juday, C. A Limnological Reconnaissance of West Okoboji. Studies in Natural History, University of Iowa, Vol. IX, No. 1, p. 1-56. Iowa City, 1920.
- Evermann, B. W. and Clark, H. W. Lake Maxinkuckee, a Physical and Biological Survey. 2 vols. Indianapolis, 1920.
- Evermann, B. W. and Cox, U. O. Report on the Fishes of the Missouri River Basin. Report U. S. Commissioner of Fish and Fisheries, p. 352-429. Washington, 1894.
- Forbes, S. A. The Food of the Smaller Fresh-water Fishes. Illinois State Laboratory of Natural History, Bull. III, Vol. 1, p. 65-94. Urbana, 1883.
- Forbes, S. A. and Richardson, R. E. The Fishes of Illinois. Natural History Survey of Illinois, Vol. III, 2nd ed. Springfield, 1920.
- Iowa Lake Bed Survey Report. Des Moines, 1917.
- Jordan, D. S. and Evermann, B. W. Fishes of North and Middle America. U. S. Nat. Mus. Bull., 47. Washington, 1896.
- Jordan, D. S. Fishes. D. Appleton and Company. New York, 1925.
- Kemmerer, George, Bouvard, J. F. and Boorman, W. R. Northwestern Lakes of the U. S. Biological and Chemical Studies with Reference to Possibilities in the Production of Fish. Bull. Bureau of Fisheries, Vol. 39, p. 51-140. Washington, 1923.
- Meek, S. E. Notes on the Fishes of Western Iowa and Eastern Nebraska. Bull. U. S. F. C., 14, p. 133-138. Washington, 1894.
- Pearse, A. S. The Distribution and Food of the Fishes of Three Wisconsin Lakes in Summer. University of Wisconsin, Studies in Science, No. 3, p. 1-61. Madison, 1921.
- Potter, G. E. The Food of the Short-nosed Garpike (*Lepidosteus platystomus*). Ia. Acad. Sci., Vol. XXX, p. 167-170. 1923.
- Shelford, V. E. Ecological Succession. I, Stream Fishes. Biol. Bull., vol. 21, p. 9-25. 1911.
- Ecological Succession. II, Pond Fishes. Biol. Bull., vol. 21, p. 127-151. 1911.
- Animal Communities in Temperate America. University of Chicago Press, Chicago. 1913.
- Shimek, Bohumil. The Plant Geography of the Lake Okoboji Region. Bull. Laboratories of Natural History, University of Iowa, Vol. VII, No. 2. Iowa City, 1915.
- Wylie, R. B. The Major Vegetation of Lake Okoboji. Proc. Ia. Acad. Sci., Vol. 27, p. 91-97. 1920.



Obtainable from the University

Editor:

Price, \$0.50



DO NOT CIRCULATE

THE UNIVERSITY OF MICHIGAN
GRADUATE LIBRARY

921 00

DATE DUE



NOV 7 1990

DEC 1 1990

JUL 28 1977
526182701

OCT 20 1978

OCT 04 1978

SEP 22 1980

AUG 4 1980



BOUL

APR 8

**UNIV. OF MICH.
LIBRARY**

UNIVERSITY OF MICHIGAN



3 9015 03554 5659

**DO NOT REMOVE
OR
MUTILATE CARD**

